115(3493)

115(349


# Proceedings of the United States National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Number 3493 1964 Volume 115, Pages 559–632


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## A REVISION OF THE CARCHARHINID SHARK GENERA SCOLIODON, LOXODON, AND RHIZOPRIONODON

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Proceedings of
the United States
National Museum

SMITHSONIAN INSTITUTION · WASHINGTON, D.C.

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# A REVISION OF THE CARCHARHINID SHARK GENERA SCOLIODON, LOXODON, AND RHIZOPRIONODON

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## Introduction

The purpose of this paper is to revise the genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. The most recent studies allocate all the species included in this report to a single genus, *Scoliodon*, and it is for this reason, together with their superficial resemblance to each other, that the three genera are treated together. While these genera do not seem to form a natural group, judgment of their relationships is deferred until the other genera of the family Carcharhinidae are more completely known.

Among the three genera, *Scoliodon* is quite distinct from the other two and easily distinguishable from all other Carcharhinidae. *Loxodon* and *Rhizoprionodon* perhaps are closely related, and it is possible that the two subgenera under *Rhizoprionodon* should be elevated to generic status. Differences separating the genera, as they are here recognized, are presented in the key, and their characteristics are discussed under the respective generic headings.

The characters previously used in assigning the species herein to a

single genus and separating them primarily from *Carcharhinus* have never been adequately evaluated. These characters are the smooth and oblique teeth, the nature of the labial furrows, and, in *Loxodon*, the presence of a spiracle (see diagnosis under *Loxodon*). In addition to these characters, and more important, I find that the group can be conveniently, though not naturally, separated from other carcharhinids in having the origin of the second dorsal fin never in advance of the middle of the anal base and frequently over or behind the anal axil. The group differs from most carcharhinids in having the cusps of most teeth smooth although in the larger specimens of some *Rhizoprionodon* species the cusps become serrulate.

These characters are not unique; a few other carcharhinids, e.g., *Carcharhinus porosus* (Ranzani) and *C. borneensis* (Bleeker), have a posteriorly placed second dorsal origin (but never posterior to a vertical line through the middle of the anal base). These species, however, have noticeably serrated teeth, the upper teeth possessing very large basal serrations on the posterior (lateral) margins, and thus differ from all the species treated in the present study. Because *Carcharhinus porosus* and *C. borneensis* lack a long upper labial furrow, they might be confused superficially with *Scoliodon laticaudus*, *Loxodon macrorhinus*, *Rhizoprionodon oligolinx*, or *R. taylori*. Aside from the nature of the teeth, *Scoliodon* (q.v.) can be distinguished by its unique fin positions; *Loxodon* (q.v.), by its short dorsal fin base, by the second dorsal fin usually originating posterior to a vertical line through the anal axil, and by having a notched orbital rim; *Rhizoprionodon oligolinx* and *R. taylori*, by having the origin of the second dorsal fin over, or posterior to, a vertical line through the posterior third of the anal base.

Several species assigned to the genus *Scoliodon* have been described from fossil teeth. I choose not to treat them here as I believe the affinities of fossils based only on teeth are at present indecipherable and possibly will remain so in most cases. This viewpoint is based on the close similarity of teeth within the living genera included in the present study, as well as a similarity to the teeth of the distantly related Sphyrnidae. The problem is further confused by the heretofore unrecognized dental sexual dimorphism that is found in several carcharhinids, including *Rhizoprionodon* and *Scoliodon*. Relationships presently based only on teeth, therefore, are open to question.

The species of *Scoliodon*, *Loxodon*, and *Rhizoprionodon* are distributed primarily through the shallow tropical marine waters of the world, with some forms straying over moderate depths and into temperate areas. None of the species is known to occur in the Mediterranean or in Oceania.

All the species treated herein, with the possible exceptions of *Rhizoprionodon terraenovae* and *R. taylori*, are used commonly as food, and one, *Scoliodon laticaudus*, is considered a delicacy. The two exceptions noted should be edible also, but they have received little attention as food, possibly because of local prejudices in the areas where they occur.

The following abbreviations have been used in the text:

AMNH—American Museum of Natural History, New York
AMS—Australian Museum, Sydney
ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History), London
CAS—California Academy of Sciences, San Francisco
CNHM—Chicago Natural History Museum
DHMB—Department of Harbors and Marine, Brisbane
DIRU—Department of Ichthyology, Rhodes University, Grahamstown, South Africa
GVF—George Vanderbilt Foundation (to be incorporated with SU—see below), Stanford, California
HUI—Hebrew University, Jerusalem, Israel
IFAN—Institute Francais d'Afrique Noire, Dakar, Senegal
IRSN—Institut Royal de Sciences Naturelles de Belgique, Brussels
ISH—Institut für Seefischeri, Hamburg
ISZZ—Institut für Spezielle Zoologie und Zoologisches Museum, Berlin
MCZ—Museum of Comparative Zoology, Harvard University
MNHN—Museum National d'Histoire Naturelle, Paris
MRAC—Musee Royal de l'Afrique Centrale, Tervuren, Belgium
NFIS—Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt
NMV—Naturhistorisches Museum, Vienna
QMB—Queensland Museum, Brisbane
RNH—Rijksmuseum van Natuurlijke Historie, Leiden
SIO—Scripps Institution of Oceanography, La Jolla
SMNS—Staatliches Museum für Naturkunde, Stuttgart
SMW—Stadtisches Museum Wiesbaden
SU—Division of Systematic Biology, Stanford University
UCLA—University of California at Los Angeles
UMML—University of Miami Institute of Marine Science
UMMZ—University of Michigan Museum of Zoology, Ann Arbor
UND—University of Natal, Durban, South Africa
UWS—University of Washington, Seattle
USNM—United States National Museum, Washington
UZMK—Universitetets Zoologiske Museum, Kobenhavn
ZSZM—Zoologisches Staatinstitut und Zoologisches Museum, Hamburg

During the course of this study, I was afforded the opportunity of examining and radiographing specimens from the collections of a large number of American and foreign institutions; I was also furnished radiographs and data on several specimens I did not see.

To my colleagues, I wish to express my gratitude for their generous aid and extreme patience: D. E. Rosen (AMNH); G. P Whitley (AMS); J. E. Böhlke (ANSP); A. C. Wheeler and G. Palmer (BMNH); W. I. Follett (CAS); L. P. Woods (CNHM); T. C. Marshall (DHMB);

J. L. B. Smith (DIRU); R. R. Rofen, A. Fehlman, and W. L. Chan (GVF); A. Ben-Tuvia (HUI); T. Monod and F. Paraiso (IFAN); J. P. Gosse (IRSN); G. Krefft (ISH); G. Deckert (ISZZ); G. W. Mead and M. Dick (MCZ); M. L. Bauchot (MNHN); M. Poll (MRAC); W. Klausewitz and F. Rössel (NFIS); P. Kähsbauer (NMV); G. Mack and A. Bartholomai (QMB); M. Boeseman (RNH); R. Rosenblatt (SIO); H. Janus (SMNS); C. Fill (SMW); G. S. Myers (SU); B. W. Walker (UCLA); C. R. Robins and W. R. Courtenay, Jr. (UMML); R. M. Bailey (UMMZ); J. D'Aubrey (UND); J. E. Randall (University of Puerto Rico); J. Nielsen (UZMK); W. Ladiges (ZSZM).

Radiographs were made in Europe and Australia with the help of the following, to whom I express my sincere appreciation: F. Meier, Roentgen Institut, Stuttgart; R. Pobisch, Tierärzliche Hochschule, Vienna; J. P. Gasc, Laboratoire d'Anatomie Comparé, Paris; Drs. Leloup and Vastesaeger, Hôpital d'Ixelles, Belgium; P. Dullemeijer and Mr. Simons, Zoologisch Laboratorium, Leiden, Holland; P. Rønne, Biofysisk Lab, Copenhagen; R. Prévôt and K. J. Thiemann, Eppendorf, Hamburg; K. L. Schmidt and R. Lingemann, St. Mallins Krankenhaus, Frankfurt; N. Mackintosh and assistants, University of Sydney; Dr. Tod and assistants, Brisbane General Hospital, Australia.

The drawings of the sharks were done by my generous colleague J. A. F. Garrick, and the shark teeth, by Dorothea B. Schultz.

Stewart Springer (no relation) read the manuscript and offered valuable criticisms.

During the course of the study I had the good fortune of having numerous discussions with, and suggestions from, J. A. F. Garrick. His perceptive comments and criticisms were of great value in improving the work and the manuscript.

This investigation was made possible by funds supplied on a contract, ONR 1354(09), between the Biology Branch of the Office of Naval Research and the Smithsonian Institution, and administered by Leonard P. Schultz. Dr. Schultz suggested the problem and greatly facilitated my work by his encouragement and his expeditious handling of the many administrative matters that arose.

## Methods and Definitions

MEASUREMENTS.—Measurements on sharks are notoriously difficult to obtain with accuracy, and it is rare that one investigator can reproduce exactly another's measurements or even his own; nevertheless, proportions based on measurements are one of the few types of characters available for the description of sharks. But many errors originate in the twisted and distorted shapes that result from

preservation procedures. The snout tip is one of the most important reference points on a shark, yet in numerous preserved specimens the tip has been pushed in, mashed, or crushed beyond reconstruction because the specimen has been forced into too small a bottle.

During the course of this study it became apparent that any given character—counts, fin shapes, fin positions, etc.—could vary widely within a species. Usually there would be at least one character in which each specimen of a particular species differed widely from all the remaining. The nature and extent of this variation was greater than I expected from my experience with teleostean fishes. For this reason, the reader should make allowances for variability when trying to fit his own specimens to my descriptions.

Total length (t.l.): Each specimen was laid on its side in a normal position on a standard fish measuring board (i.e., the caudal fin was not stretched to its fullest extent toward the midline of the body axis but was placed at what appeared to be its normal angle to the body). The total length is the distance from the tip of the snout (along the projected midline of the body axis) to a point on a vertical line through the tip of the upper lobe of the caudal fin.

This measurement contains two errors: (1) Because a shark in contour has a broad head and a narrow tail, the sagittal plane of its body is not parallel to the measuring board when the side of the shark is laid flat on the board. The total length measured along this inclined plane is shorter than the total length measured when the tail of the specimen is raised to make the sagittal plane parallel to the measuring board. The amount of error depends on the relative thicknesses of the head and tail.

(2) Total lengths of various sized specimens cannot be measured comparably because in many of the larger specimens there is a tendency for the axis of the upper caudal lobe to become raised in relation to the horizontal axis of the body. Thus, proportional measurements based on total lengths of large specimens appear greater than those based on the total lengths of smaller specimens, which may not actually be the case. (The angle also varies somewhat in sharks of the same size.)

Snout tip to—

outer nostrils: A straight pencil line was drawn between the anterior margins of each nostril. One point of a pair of dividers was placed on the tip of the snout and the other on the center of the line. The distance between the two points of the dividers was measured.

eye: Pencil lines were extended ventrally from the anterior rim of each orbit and joined on the underside of the head. One point of the dividers was placed on the tip of the snout and the other on the center of the line. The distance between the two points of the dividers was measured.

mouth: One point of the dividers was placed on the tip of the snout and the other on the tip of the lower jaw. The distances between the two points was measured.

gill-opening: (This and the next seven measurements were made with the specimen lying on its side on the measuring board.) A line was drawn across the underside of the head connecting the first gill-opening of each side at the point of its junction with the body. A right-angled triangle was placed vertically on the measuring board with the vertical edge crossing the midpoint of the line. The distance measured was the point where the base of the triangle intersected the scale on the measuring board.

pectoral origin: I found the origin of each pectoral fin by pressing my thumbnail at the junction of the anterior margin of that fin with the body and by locating the point of insertion of the hard internal element comprising that margin. This point on each fin was connected with a line across the ventral surface of the specimen, and the midpoint of this line was crossed by the edge of the triangle as above. The distance measured was the point where the base of the triangle intersected the scale on the measuring board. Frequently, because of deformities or poor preservation, one point of origin was much in advance of the other. By measuring the distance to the midpoint of the connecting line, I obtained the approximate distance to the true origin.

pelvic origin: This was determined and measured in a way similar to that of the pectoral origin.

first dorsal origin: The origin was found in the same manner as that used for the pectorals and pelvics. A line perpendicular to the measuring board (parallel to the anterior end of the board) was extended ventrally over the side of the shark and the vertical edge of the triangle was placed on this line; the distance along the measuring board was recorded.

second dorsal origin: The second dorsal origin is a difficult point to establish and can vary considerably with each investigator. I used the point which I subjectively considered to be the point where the sharp anterior edge of the fin first faded out as it passed into the dorsal body contour. A line was drawn ventrally from this point and the distance to it measured in the same manner as it was done for the first dorsal fin.

anal origin: This was determined and measured in the same manner as for the second dorsal origin except that it was necessary only to mark the origin and to place the vertical edge of the triangle on it.

upper caudal origin: This origin was determined to be at the point where the comparatively thin anterior dorsal edge of the upper

caudal lobe faded into the dorsal body contour. The point is usually close to the posterior end of the upper precaudal pit. A line was extended ventrally, and, using the triangle, I measured the distance to this line.

lower caudal origin: This was obtained in a way similar to that used for the upper caudal origin except that it was necessary only to mark the origin.

Distance between the inner corners of the nostrils: Measured as the least distance between the two nostrils.

Mouth width: The distance between the corners of the mouth.

Mouth length: The distance from the tip of the lower jaw to the midpoint of a line connecting the corners of the mouth.

Upper labial furrow length: The distance from the anterior end of the upper furrow to the posterior tip of the fold formed by the furrow.

Lower labial furrow length: The distance from the anterior end of the lower furrow to the posterior tip of the fold formed by the upper furrow.

Gill-opening length: Measured by placing the divider points at the dorsal and ventral points of junction of the gill-opening with the body.

Eye diameter: The length of the horizontal diameter of the rim of the orbit.

First dorsal fin, second dorsal fin, and anal fin—

total length: Measured from the origin to the tip of the posterior margin of the fin. This measurement usually is slightly smaller than the sum of the next two measurements because of the difficulty of determining the exact anterior margin of the axil.

length of base: Measured from the origin to the axil. The latter point is determined by raising the posterior margin of the fin and placing one point of the dividers on the most posterior extension of the base. This point is somewhat posterior to the anteriorly extending furrow of the posterior margin.

length of posterior margin: The distance from the axil to the posterior tip of the fin.

height: A measurement perpendicular to the base of the fin made by placing one point of the dividers at the axil and the other at an imaginary point on the level of the tip of the anterior margin of the fin.

Pectoral and pelvic fins—

inner corner: The angle formed by the junction of the distal and posterior margins of the fin.

length of base: Measured in same manner as the vertical fins above.

length of anterior margin: Measured as the length of a straight line from the origin to the most distal point on the anterior margin of the fin.

length of distal margin: Measured as the length of a straight line from the most distal point on the anterior margin to the tip of the inner corner.

Pectoral width: Measured as the length of a line perpendicular to the anterior margin and extending to the tip of the inner corner.

Clasper length: Measured as the distance between the two points of a pair of dividers with one point in the axil of the pelvic fin and the other on the tip of the clasper.

During the course of this study I noticed the lack of male specimens with developing claspers. All males I examined had either juvenile or completely formed claspers. Plotting clasper lengths (as percent t.l.) against total length (see species accounts) established this impression. An explanation of the phenomenon probably lies in the fact that claspers do not mature gradually with the growth of the individual. Their growth to maturity begins abruptly and is completed in a very brief period of time and generally simultaneously within a given population (year class) of males. Some males with intermediately developed claspers undoubtedly will be collected, but only few in comparison with those having juvenile or completely developed claspers. Thus, puberty in males is of a much shorter duration than periods of complete immaturity or maturity. Heath (1960) noted that the claspers of *Squalus acanthias* and *Mustelus canis* mature rapidly with little increase in body length at time of maturation.

Caudal fin—

length of the upper lobe: Measured as the length of a straight line from the upper caudal origin to the distal tip of the upper lobe.

length of the lower lobe: Measured as the length of a straight line from the lower caudal origin to the distal tip of the lower lobe.

dorsal tip to notch: Measured as a straight line from the tip of the upper lobe to the distal tip of the notch.

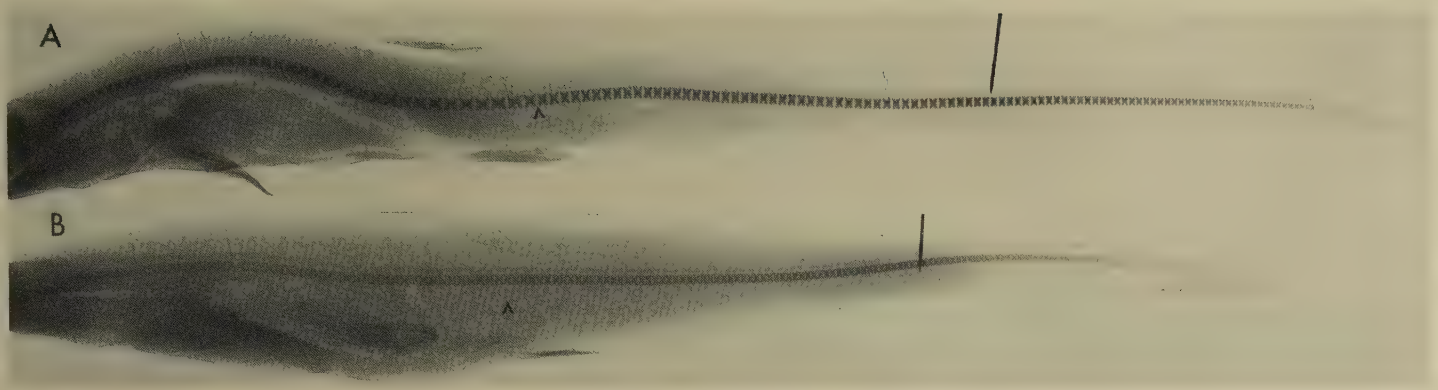
notch depth: Measured from the distal tip of the notch to the proximal end of its incision.

Dorsal-pectoral ratio.—This ratio is found by dividing the total length of the first dorsal fin by the length of the anterior margin of the pectoral fin and multiplying by one hundred (table 3).

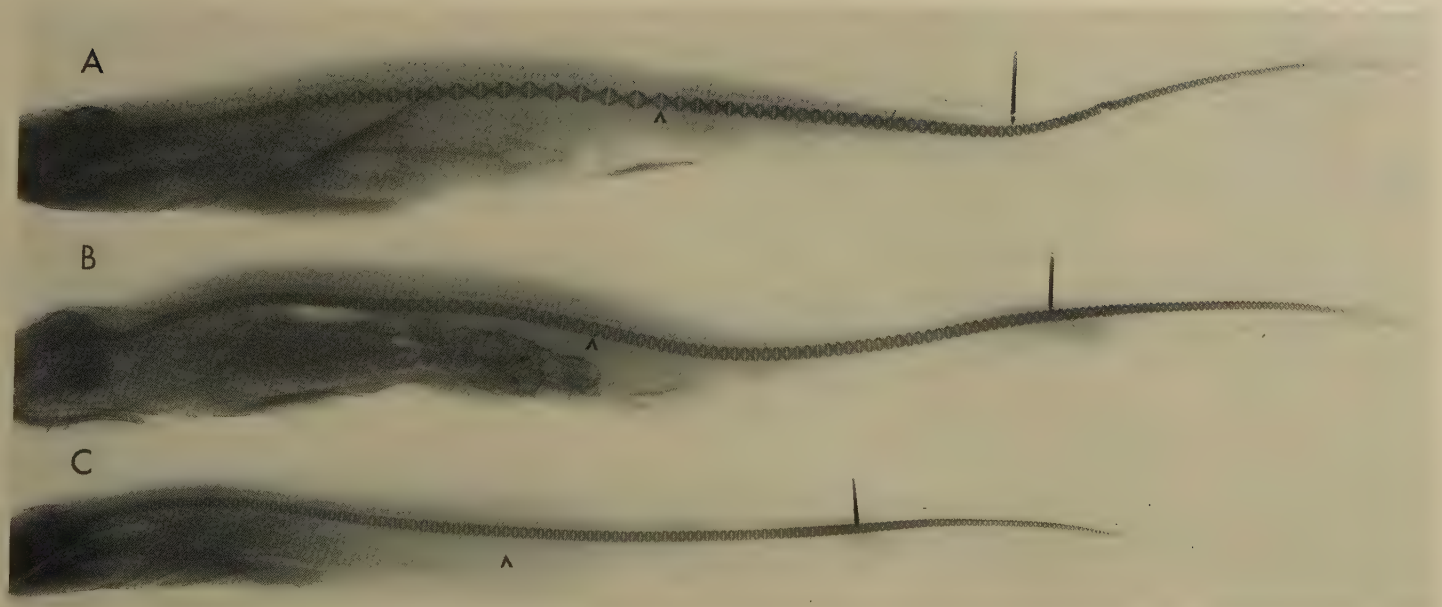
Counts.—Teeth: In this study only the upper jaw is considered to have a symphysial tooth, and there is always one, never more. The teeth on the outer margin of each jaw form a "row" and a single tooth of the row with those teeth aligned inward to it comprise a "series."

It was found that total counts of teeth in a row of either jaw gave more constant results than counts from a single ramus of either jaw.

The most posterior teeth of a ramus frequently are very small




RADIOGRAPHS.—Figure A: *Loxodon macrorhinus*, SU 26819, embryo, Oriental Negros, Philippine Islands (caret indicates presumable point where diplospondyli begins; pin indicates separation of precaudal from caudal vertebrae); Figure B: *Scoliodon laticaudus*, SU 32434, Chusan Island, Tinghai, China (caret indicates presumable region where diplospondyli begins; pin indicates separation of precaudal from caudal vertebrae).




RADIOGRAPHS.—Figure A: *Rhizoprionodon terraenovae*, USNM 125873, Mobile Bay, Alabama (caret indicates presumable point where diplospondyli begins; pin indicates separation of precaudal from caudal vertebrae); Figure B: *Rhizoprionodon lalandei*, USNM 100811, Bandeirantes, Brazil (caret indicates presumable point where diplospondyli begins; pin indicates separation of precaudal from caudal vertebrae); Figure C: *Rhizoprionodon oligolinx*, SU 41986, Calcutta, India (caret indicates presumable region where diplospondyli begins; pin indicates separation of precaudal from caudal vertebrae).

(sometimes a series consists of a single tooth) and extremely difficult to count. Competent colleagues, not engaged in elasmobranch studies, were given specimens on which to count the teeth and more often than not made significant errors. Caution, as well as magnification and good illumination, is recommended strongly for such counts.

Enlarged hyomandibular pores: In the genus *Rhizoprionodon*, there is a discrete group of comparatively large and noticeable pores of the hyomandibular series opening near the upper labial furrow and extending dorsoposteriorly a short distance (see figures of the various species). Frequently these pores are in a straight line, sometimes irregularly biserial. Some difficulty in counting was found when the pores were clogged or when they had not broken through the denticles (in small specimens). Counts should be made under magnification and any large gaps between pores should be searched for obscured members of the series. Sometimes the most anterior pore is well separated from the remaining ones. *Scoliodon* may have a few enlarged pores, but they are frequently difficult to find. (See also description of *Loxodon*.)

Vertebrae: Radiographs of sharks were made using a very fine-grain industrial film. The vertebral count was separated into two parts: (1) precaudal vertebrae, which includes all complete centra anterior to the forward edge of the upper precaudal pit; (2) caudal vertebrae, which includes those centra posterior to the precaudal vertebrae.

Precaudal vertebral counts are sometimes subject to an error of plus or minus two vertebrae. One reason for this is that to establish accurately the position of the first vertebra is not always possible because of masking by other structures behind the head, including the occipital condyles. Another is that sometimes an error in establishing the last precaudal vertebra occurs because of the angle with which the X-rays entered the body in the region of the precaudal pit; a two-dimensional parallax is created on the film. This last problem was circumvented in most instances by sticking a pin, to mark the first caudal vertebra, into the vertebral column immediately posterior to the anterior margin of the precaudal pit. The errors affect the counts very little.

At the tip of the caudal fin the last few vertebrae are frequently and irregularly fused (each fusion was counted as one vertebra), or they are too small to give good resolution on the film. Caudal vertebral counts were made under high illumination and magnification, and they are reasonably accurate for the purposes of this study.

In embryos, precaudal vertebrae are formed early, but caudal vertebrae are not completely formed until shortly before birth; therefore, precaudal, but not caudal, vertebral counts from embryos can be used (in *Loxodon*, for which I had few specimens, caudal counts

of embryos were used). In those instances wherein several embryonic siblings or an embryo and its mother were available, none of the embryonic counts are reported in the tables. If only the embryo was available, the body count was included.

In the genus *Loxodon* and the type subgenus of *Rhizoprionodon*, the precaudal centra become gradually and markedly elongate (plates 1 and 2) to a point above the region between the anus and posterior pelvic base, where they become abruptly reduced in length. The point at which reduction occurs is presumably the point where diplospondyly begins. In *Scoliodon* and the subgenus *Protozygaena* (plates 1 and 2), the precaudal centra remain more or less constant in length and the point at which reduction takes place is noticeable only on close scrutiny. Sometimes the diplospondyly is irregular with elongate and reduced centra interspersed over a short distance.

## Key to *Scoliodon*, *Loxodon*, and *Rhizoprionodon*

(Characters separating these three genera from other carcharhinid genera are discussed in the introduction; characters delimited in the key are not repeated in the generic or specific diagnoses and descriptions unless necessary.)

1a. Posterior tip of first dorsal fin extending to, or beyond (usually), a vertical line through the midbase of pelvic fin; origin of pectoral fin below, or only slightly in advance of, fifth-gill opening; distal tip of appressed pectoral fin over, or anterior (usually) to, its inner corner; snout tip to first dorsal origin 34.7–40.8 percent of total length; length of gill-openings equal to, or greater (usually) than, horizontal eye diameter; length of anal base 6.9–8.4 percent of total length; number of precaudal vertebrae exceeding number of caudal vertebrae by 43–57 (one specimen out of 98 had only 35 more precaudal vertebrae than caudal vertebrae) (Indo-Pacific).
**Scoliodon laticaudus**

1b. Posterior tip of first dorsal fin never extending much, if any, beyond a vertical line through the origin of pelvic fin; origin of pectoral fin below fourth to third gill-opening; distal tip of appressed pectoral fin posterior to its inner corner; snout tip to first dorsal origin 27.0–34.0 percent of total length; length of one or more gill-openings less than horizontal eye diameter; length of anal base 3.3–5.4 percent of total length; number of precaudal vertebrae ranging from 18 less than to 26 more than number of caudal vertebrae . . . . . 2

2a. Posterior rim of orbit with a slight notch at midlevel; origin of dorsal fin posterior to appressed pectoral inner corner by a distance greater than length of the fourth gill opening; eye larger at all sizes (compare table 6 with tables 4, 10, 11, 13–17); mouth small, its width 4.9–5.9 percent of total length; its length 3.1–4.2 percent of total length; base of first dorsal fin 6.2–7.6 percent of total length; lengths of upper and lower labial furrows combined is less than 1.5 percent of total length (Indo-Pacific).
**Loxodon macrorhinus**

2b. Posterior rim of orbit without a notch; origin of dorsal fin rarely posterior to appressed pectoral inner corner by a distance as great as length of fourth gill-opening, usually over, or in advance of, appressed pectoral inner corner; eye smaller at all sizes; mouth larger, its width 6.2–7.8 percent of

TABLE 1.—*Frequency distribution of total teeth in outer row*

| | Upper jaw | | | | | | | | | | | Lower jaw | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 |
| *S. laticaudus* | – | – | 3 | 6 | 35 | 10 | 26 | 6 | 3 | – | 1 | – | – | – | 2 | 5 | 17 | 12 | 31 | 5 | 13 | 1 | 2 | – | 2 |
| *L. macrorhinus* | – | – | 13 | 2 | 3 | 1 | – | – | – | – | – | – | – | – | 3 | 1 | 12 | 3 | 2 | – | – | – | – | – | – |
| *R. longurio* | – | – | – | – | 16 | 2 | 13 | 1 | – | – | – | – | – | – | – | – | 21 | 2 | 9 | – | – | – | – | – | – |
| *R. acutus* | 1 | – | 63 | 4 | 7 | – | – | – | – | – | – | – | 1 | 2 | 66 | 1 | 4 | – | – | – | – | – | – | – | – |
| *R. terraenovae* | – | 1 | 18 | – | 1 | – | – | – | – | – | – | – | – | – | 18 | 1 | 1 | – | – | – | – | – | – | – | – |
| *R. porosus* | – | 1 | 19 | 1 | 1 | – | – | – | – | – | – | – | – | – | 22 | – | – | – | – | – | – | – | – | – | – |
| *R. lalandei* | – | – | 21 | – | – | – | – | – | – | – | – | – | – | 2 | 19 | – | – | – | – | – | – | – | – | – | – |
| *R. oligolinx* | 30 | 6 | 19 | – | – | – | – | – | – | – | – | 1 | 42 | 4 | 8 | – | – | – | – | – | – | – | – | – | – |
| *R. taylori* | 8 | 1 | – | – | – | – | – | – | – | – | – | 1 | 8 | – | – | – | – | – | – | – | – | – | – | – | – |

| | Both jaws | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 |
| *S. laticaudus* | – | – | – | – | – | 2 | – | 4 | 5 | 11 | 12 | 12 | 8 | 12 | 6 | 9 | 3 | 2 | 1 | 1 | 1 | – | – | 1 |
| *L. macrorhinus* | – | – | – | – | – | 3 | 1 | 9 | 1 | 1 | 1 | 3 | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. longurio* | – | – | – | – | – | – | – | – | – | 16 | 2 | 3 | 2 | 8 | 1 | – | – | – | – | – | – | – | – | – |
| *R. acutus* | – | – | – | 2 | 2 | 59 | 2 | 6 | 1 | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. terraenovae* | – | – | – | – | 1 | 16 | 1 | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. porosus* | – | – | – | – | 1 | 19 | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. lalandei* | – | – | – | – | 2 | 19 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. oligolinx* | 1 | 28 | 6 | 9 | 4 | 7 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. taylori* | 1 | 7 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |

TABLE 2.—*Frequency distribution of number of precaudal vertebrae minus number of caudal vertebrae*

| | Minus | | | | | | Plus | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 19–17 | 16–14 | 13–11 | 10–8 | 7–5 | 4–2 | 1–0–1 | 2–4 | 5–7 | 8–10 | 11–13 | 14–16 | 17–19 | 20–22 | 23–25 | 26–28 | 29–31 | 32–34 | 35–37 | 38–40 | 41–43 | 44–46 | 47–49 | 50–52 | 53–55 | 56–58 |
| *S. laticaudus* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 5 | 18 | 30 | 29 | 11 | 4 |
| *L. macrorhinus* | – | – | – | – | – | – | 1 | 2 | 6 | 7 | 1 | – | 1 | – | 3 | 1 | – | – | – | – | – | – | – | – | – | – |
| *R. longurio* | – | – | 1 | – | 1 | 9 | 12 | 7 | 2 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. acutus* | 1 | 7 | 24 | 36 | 28 | 27 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. terraenovae* | 2 | 8 | 26 | 28 | 7 | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. porosus* | – | 3 | 9 | 25 | 14 | 7 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. lalandei* | – | – | – | – | – | – | – | – | 2 | 13 | 15 | 12 | 2 | 1 | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. oligolinx* | – | – | – | – | – | – | – | – | 2 | – | 4 | 19 | 20 | 5 | 2 | – | – | – | – | – | – | – | – | – | – | – |
| *R. taylori* | – | – | – | – | – | – | – | – | – | 2 | 4 | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |

TABLE 3.—*Frequency distribution of dorsal-pectoral ratios (total length of first dorsal fin divided by length of pectoral anterior margin times 100)*

| | 80–81 | 82–83 | 84–85 | 86–87 | 88–89 | 90–91 | 92–93 | 94–95 | 96–97 | 98–99 | 100–101 | 102–103 | 104–105 | 106–107 | 108–109 | 110–111 | 112–113 | 114–115 | 116–117 | 118–119 | 120–121 | 122–123 | 124–125 | 126–127 | 128–129 | 130–131 | 132–133 | 134–135 | 136–137 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. laticaudus* | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 2 | 3 | 2 | 3 | 7 | 1 | 3 | 3 | 3 | 1 | 3 | 1 | 1 | 1 | – | 2 |
| *L. macrorhinus* | 1 | 2 | 3 | 3 | 2 | 4 | 2 | 2 | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. longurio* | – | – | – | – | – | – | 3 | 1 | – | 1 | 5 | 4 | 4 | 2 | 2 | 2 | 2 | 1 | 1 | 4 | – | – | – | – | – | – | – | – | – |
| *R. acutus* | – | – | – | – | – | 5 | 1 | 2 | 8 | 7 | 22 | 16 | 16 | 12 | 9 | 3 | – | 1 | – | – | – | – | – | – | – | – | – | – | – |
| *R. terraenovae* | 1 | – | – | 2 | 3 | 3 | 5 | 6 | 9 | 3 | 2 | 1 | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. porosus* | – | – | 2 | – | 6 | 3 | 6 | 7 | 5 | 3 | 2 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. lalandei* | – | – | – | – | – | – | – | – | – | – | 1 | – | 4 | 3 | 5 | 6 | 1 | – | 5 | – | 6 | 2 | – | – | – | – | – | – | – |
| *R. oligolinx* | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 | 2 | 8 | 4 | 6 | 7 | 2 | 8 | 4 | 3 | 1 | – | | – | – | – | – |
| *R. taylori* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 | – | 1 | 4 | 1 | – | – | – | – | – | – | – |

total length: its length 4.1–5.3 percent (usually more than 4.2 percent) of total length; base of first dorsal fin 7.8–10.9 percent of total length (only one specimen out of 70 below 8.3 percent); lengths of upper and lower labial furrows combined is more than 1.5 percent of total length.

**3 Rhizoprionodon**

3a. Upper labial furrow short or virtually absent, 0–1.3 percent of total length (rarely more than 1 percent), usually shorter than lower labial furrow; teeth modally fewer (see tables 1–3) . . . . . 4

3b. Upper labial furrow longer, always present, more than 1.1 percent of total length (usually more than 1.3 percent), rarely shorter than lower labial furrow; teeth modally more (see tables 1–3) . . . . . 5

4a. Total enlarged hyomandibular pores on both sides of head 7–16 (only 2 of 54 specimens with more than 14); precaudal vertebrae 84–91 (Indo-Pacific north of Australia) . . . . . **Rhizoprionodon oligolinx**

4b. Total enlarged hyomandibular pores on both sides of head 15–22; precaudal vertebrae 73–80 (Australia) . . . . . **Rhizoprionodon taylori**

5a. Total teeth in outer row of both jaws 53–58; total teeth in outer row of lower jaw 26–28; total teeth in outer row of upper jaw 27–30; snout tip to outer nostrils usually longer at any given size (fig. 1), ranging from 4.5–6.0 percent of total length (Eastern Pacific) . . . **Rhizoprionodon longurio**

5b. Total teeth in outer row of both jaws 47–53 (only 2 specimens out of 74 of *R. acutus* with 53); total teeth in outer row of lower jaw 22–26 (only 1 specimen out of 19 of *R. terraenovae* and 4 of *R. acutus* with 26); total teeth in outer row of upper jaw 23–27 (1 specimen each of *R. porosus* and *R. terraenovae* and 7 of *R. acutus* with 27); snout tip to outer nostrils usually shorter at any given size (fig. 1), 3.2–4.5 percent of total length in *R. porosus* and *R. terraenovae*, 4.4–5.1 percent in *R. lalandei*, 4.0–5.4 percent in *R. acutus* (other than Eastern Pacific) . . . . . 6

6a. Tip of appressed pectoral fin fails to reach level of middle of first dorsal base; dorsal-pectoral ratio 100–123 (only 1 out of 33 specimens with less than 105); clasper length 5.9 percent or more of total length in males 500 mm. or larger; largest specimen seen: 640 mm.; precaudal vertebrae 79–90 (rarely less than 84), outnumbering caudal vertebrae 5–20 (usually 7 or more); centra in posterior monospondylous region scarcely longer than those in anterior diplospondylous region (pl. 2B) (Western Atlantic). **Rhizoprionodon lalandei**

6b. Tip of appressed pectoral fin reaches to, or beyond, level of middle of first dorsal base (for dorsal-pectoral ratio, see 7a and 7b); clasper length 3.9 percent or less in males less than 620 mm.; attaining a length of over 1000 mm.; precaudal vertebrae 55–79, equal to, or fewer in number than, caudal vertebrae (one specimen of *R. acutus* with one more caudal vertebra than body vertebrae); centra in posterior monospondylous region markedly longer than those in anterior diplospondylous region (pl. 2A) . . . . . 7

7a. Snout tip 4.0–5.4 percent of total length, usually greater at any given size (fig. 1); dorsal-pectoral ratio usually larger (91–114, most specimens 100 or more, table 3) (Africa to Australia) . . . . . **Rhizoprionodon acutus**

7b. Snout tip 3.2–4.5 percent of total length, usually smaller at any given size (fig. 1); dorsal-pectoral ratio usually smaller (81–104, few specimens over 100, table 3) (Western Atlantic) . . . . . 8

8a. Precaudal vertebrae 58–66 (1 specimen out of 74 with 66, North Carolina) (Atlantic and Gulf coasts of the United States and Mexico). **Rhizoprionodon terraenovae**

8b. Precaudal vertebrae 66–75 (2 specimens out of 58 with 66, Brazil) (Western Atlantic except United States and Mexico) . . **Rhizoprionodon porosus**

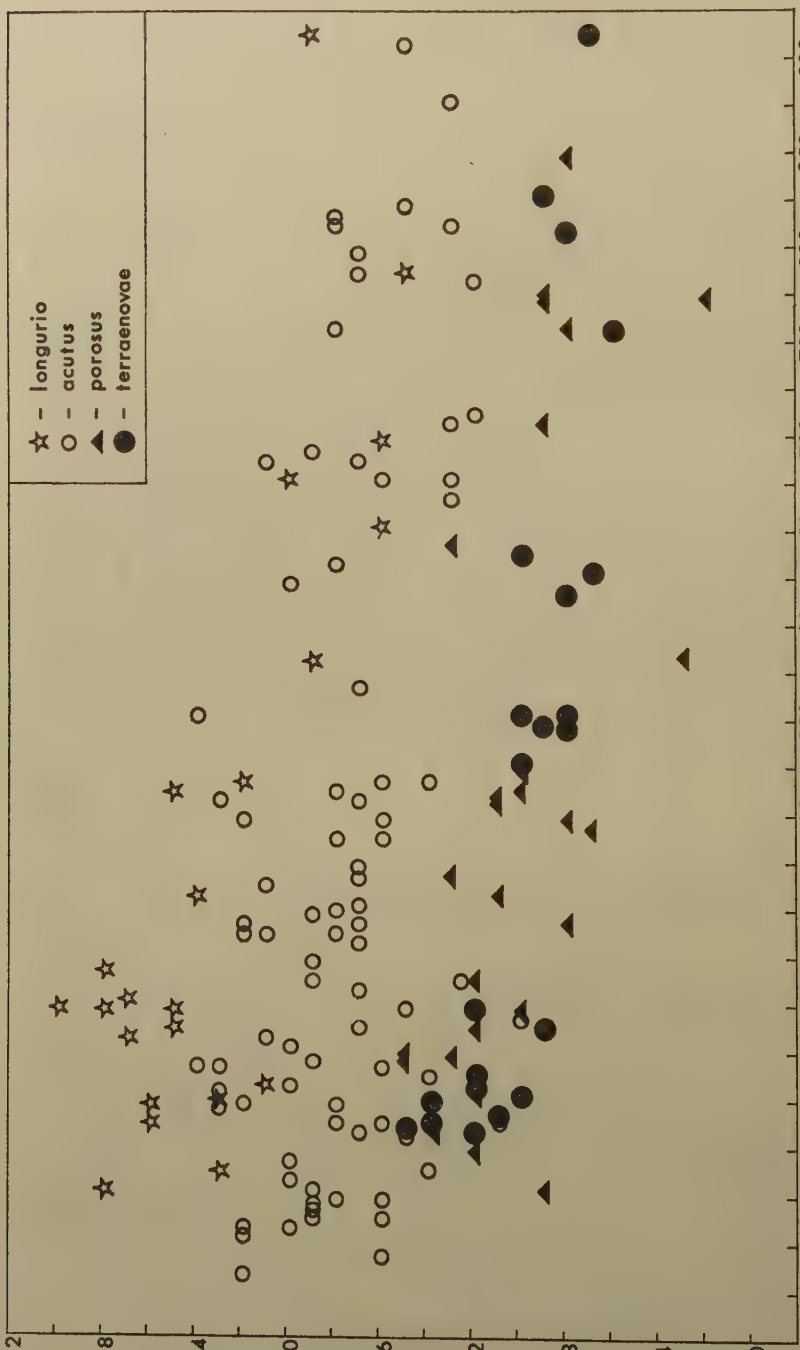



FIGURE 1.—Snout tip to outer nostrils as percent of total length versus total length in the subgenus *Rhizoprionodon*.

## *Scoliodon* Müller and Henle

*Scoliodon* Müller and Henle, 1837, Sitzb. Akad. Wiss. Berlin, p. 114 (name only).

*Scoliodon* Müller and Henle, 1837, Arch. Naturg., vol. 3, no. 1, p. 397 (name and diagnosis).

*Scoliodon* Müller and Henle, 1838, L'Institut, vol. 6, no. 244, p. 64 (name and diagnosis).

*Scoliodon* Müller and Henle, 1838, Mag. Nat. Hist., new. ser., vol. 2, p. 35 (name and diagnosis).

*Scoliodon* Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen, 2nd page 27 (a subgenus with three included species; type species *Carcharias* (*Scoliodon*) *laticaudus* Müller and Henle, by subsequent designation, Gill, 1862, Ann. New York Lyc., vol. 8, p. 401).

*Physodon* Valenciennes *in* Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen, p. 30 (a subgenus; type species *Carcharias* (*Physodon*) *mülleri* Valenciennes by monotypy).

In several copies of Müller and Henle (1841), except that in the British Museum, seen by me, there are two pages numbered 27 and two numbered 28. The first page 27 lists *Scoliodon* as a new genus and the description terminates and is complete at the bottom of the first page 28. The second page 27 lists *Scoliodon* as a subgenus and the description continues from page 28 to page 29. Obviously, the first pair of pages were not meant to be included and their elimination from the text causes no discontinuity. This is not so with the second pair. For nomenclatural purposes I disregard the first pages 27 and 28.

Bigelow and Schroeder (1948, p. 292) included in their synonymy of *Scoliodon* (which embodies all three genera treated in my study) the genus *Cynocephalus* (not *Cynocephalus* Gill, 1862) which they attributed to Bleeker (1879). They designated *Carcharias* (*Scoliodon*) *macrorhynchus* Bleeker (1852, but 1858 in their work) as type species. However, Bleeker (1878) first used the name *Cynocephalus* for a group of shark species that did not include *C.* (*S.*) *macrorhynchus;* therefore, Bigelow and Schroeder were in error in dating the genus from 1879 and *C.* (*S.*) *macrorhynchus* could not be designated as type species for the genus.

*Cynocephalus* was first used validly in 1768 for a genus of mammals; Bleeker's usage of the name was apparently an extrapolation from Gill (1862), who gave a key to shark genera and designated *Squalus glaucus* Linnaeus as type species of *Cynocephalus*, listing no other species. For these reasons, I do not believe Bleeker was creating a genus, and future workers should refrain from selecting a type from Bleeker and erecting an additional junior homonym.

Diagnosis.—Small sharks (largest specimen seen 581 mm. t.l.) distinct from all other Carcharhinidae in having the tip of the posterior margin of the first dorsal fin extending posteriorly beyond the level of

the origin of the pelvic fin to a point over, or beyond (usually), the middle of the pelvic base; distinct from all Carcharhinidae except *Aprionodon isodon, Carcharhinus oxyrhynchus,* and *C. temmincki* in having the origin of the pectoral fin below, or only slightly in advance of, the level of the fifth gill-opening. Differing from most Carcharhinidae in having the outer tip of the appressed pectoral fin over, or in advance of, its inner corner and from all Carcharhinidae in having both the tip and inner corner well in advance of the level of the origin of the first dorsal fin. The origin of the second dorsal fin ranges from above the posterior third of the anal base to over the anal axil. It is usually over the posterior fifth of the anal base.

A single common species distributed from the coasts of Japan and southeast Asia to India and the Dutch East Indies, exclusive of New Guinea, and absent also from Australia, the Philippines, and Oceania. At the present time I know of no close relative to this genus among the other carcharhinid genera.

### *Scoliodon laticaudus* Müller and Henle

FIGURES 2, 3; PLATE 1B

"Pala Sorra" Russell, 1803, Descriptions and figures of two hundred fishes . . . Coromandel, vol. 1, p. 9, fig. 14 (a common name).

*Carcharias* (*Scoliodon*) *laticaudus* Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen, p. 28, pl. 8 (India).

*Carcharias* (*Physodon*) *mülleri* Valenciennes *in* Müller and Henle, 1841, ibid., p. 30, pl. 19, fig. 1 (Bengal).

*Carcharias* (*Scoliodon*) *macrorchynchos* Bleeker, 1852, Verh. Bataviaasch Gen., vol. 24, p. 31, pl. 1, fig. 1 (Batavia, spelled *macrorhynchos* in other parts of the paper and in subsequent literature).

*Carcharias palasorra* Bleeker, 1853, Verh. Bataviaasch Gen., vol. 25, p. 9 (Coromandel, based on "Pala Sorra" Russell, see discussion below).

DIAGNOSIS.—Distinctive characters are those of the genus (p. 568).

DESCRIPTION (see also table 4).—Body vertebrae 97–112 (table 5), centra not markedly elongate in posterior monospondylous region (pl. 1B); caudal vertebrae 50–62, total vertebrae 148–171; teeth smooth-edged, upper teeth 12–1–12 to 16–1–16; lower teeth 12–12 to 17–17 (higher, or lower, counts in upper and lower jaws correlated); enlarged hyomandibular pores 0–5 on each side of head (rarely more than 2; frequently difficult to see).

Denticles imbricate, 3-ridged and 3-toothed in young, 3- to 5-ridged and 3- to 4-toothed in adults.

Color of preserved specimens: Buff brown, purplish brown, or gray brown, darker above, pale below; fins sometimes darker than body; edges of fins at all sizes without dark margins except sometimes the dorsal and distal edges of the upper caudal lobe; in adult males the distal third of clasper abruptly paler than remainder.

The appearance of this species is most striking for its comparatively long and greatly depressed snout (snout in front of nostrils is up to 7.0 percent of t.l. and almost always more than 5.4 percent).

The upper labial furrow is developed poorly and exists only as a short crease directed at a right angle from the lower furrow, which is visible when the mouth is closed.

There is no interdorsal ridge and the lower precaudal pit is essentially obsolete.

Growth changes (see table 4): Snout length to outer nostrils, eye, mouth, first gill-opening, pectoral origin, and pelvic origin tend to decrease in percent of t.l. with increased t.l., as do distance between inner nostrils, mouth width, gill-opening lengths, and eye diameter. Height of first dorsal fin, anterior and distal margins of pectoral fin, width of pectoral fin and distance from tip of caudal fin to notch tend to increase with increased t.l.

In the largest specimens examined the axis of the upper caudal lobe has been raised in relation to the horizontal axis of the body as compared with the condition in small specimens (even including mature individuals; see fig. 2).

Males may mature at about 350 mm. t.l. as determined by what appears to be a fully developed clasper (when the clasper is about 8 percent of t.l.). The following tabulation for *Scoliodon* indicates that claspers gradually increase in proportionate length until the shark reaches about 350 mm. t.l. The clasper lengths then increase abruptly and remain more or less constant in proportionate length until the shark is about 450 mm. t.l. At this point there is a gradual decrease in proportionate clasper length.

| *Locality* | *T.L.* | *Clasper Length (%)* | *Locality* | *T.L.* | *Clasper Length (%)* |
|---|---|---|---|---|---|
| India | 126 | 2.9 | China | 344 | 2.9 |
| India | 165 | 2.4 | Malaya | 352 | 8.5 |
| India | 167 | 2.7 | China | 360 | 2.8 |
| India | 174 | 2.9 | India | 378 | 9.8 |
| India | 176 | 2.3 | India | 389 | 8.8 |
| India | 185 | 2.9 | Malaya | 392 | 8.9 |
| China | 188 | 2.2 | India | 423 | 9.2 |
| India | 207 | 3.5 | Ceylon | 426 | 9.4 |
| India | 236 | 3.0 | India | 455 | 9.6 |
| India | 238 | 4.0 | India | 484 | 7.7 |
| India | 240 | 3.7 | India | 506 | 8.9 |
| India | 257 | 4.2 | China | 581 | 8.1 |

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TABLE 4.—*Proportional dimensions in percent of total length of* Scoliodon laticaudus

| | ♀ 153 mm. India SU 41984 | ♂ 165 mm. India SU 41984 | ♂ 207 mm. India SU 41983 | ♀ 228 mm. China USNM 86334 | ♀ 277 mm. China SU 32434 | ♀ 323 mm. China SU 32434 | ♂ 352 mm. Malaya SU 38377 | ♂ 378 mm. India SU 41982 | ♀ 460 mm. India SU 14444 | ♀ 462 mm. China SU 13969 | ♂ 484 mm. India MNHN 1041 [1] | ♀ 518 mm. India MNHN 1123 [2] | ♀ 542 mm. India USNM 196135 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | | | | |
| outer nostrils | 6.8 | 7.0 | 6.3 | 6.4 | 6.9 | 6.2 | 5.7 | 5.6 | 5.6 | 6.3 | 5.2 | 6.1 | 6.0 |
| eye | 10.5 | 11.2 | 10.4 | 9.6 | 10.8 | 9.9 | 9.4 | 9.0 | 8.7 | 9.6 | 7.8 | 8.5 | 8.9 |
| mouth | 10.5 | 11.2 | 9.6 | 9.2 | 10.5 | 9.6 | 8.8 | 8.2 | 8.3 | 9.1 | 7.4 | 8.7 | 8.7 |
| 1st gill-opening | 22.8 | 23.6 | 20.8 | 19.7 | 21.3 | 18.9 | 18.8 | 17.5 | 18.0 | 18.8 | 16.1 | 17.0 | 18.4 |
| pectoral origin | 27.4 | 28.4 | 25.2 | 24.6 | 25.2 | 24.2 | 23.6 | 21.7 | 22.4 | 22.5 | 20.9 | 22.4 | 24.6 |
| pelvic origin | 47.1 | 49.6 | 47.8 | 47.8 | 48.8 | 46.9 | 45.4 | 45.8 | 47.4 | 44.8 | 44.4 | 45.8 | 47.0 |
| 1st dorsal origin | 40.5 | 40.6 | 39.2 | 40.8 | 37.8 | 37.4 | 36.4 | 36.5 | 35.8 | 35.7 | 34.7 | 35.1 | 37.8 |
| 2nd dorsal origin | 66.7 | 66.0 | 65.7 | 66.7 | 66.1 | 65.5 | 66.7 | 66.3 | 65.7 | 64.5 | 65.4 | 64.9 | 68.4 |
| anal fin origin | 61.5 | 60.6 | 62.3 | 60.5 | 60.3 | 58.8 | 60.0 | 59.4 | 60.5 | 57.7 | 59.5 | 59.4 | 61.4 |
| upper caudal origin | 79.0 | 78.6 | 77.7 | 78.5 | 77.6 | 76.8 | 76.1 | 76.2 | 78.9 | 77.0 | 79.7 | 77.4 | 79.0 |
| lower caudal origin | 75.8 | 76.4 | 75.8 | 75.5 | 74.7 | 74.4 | 74.2 | 73.2 | 75.6 | 74.5 | 76.0 | 75.0 | 76.0 |
| Nostrils: | | | | | | | | | | | | | |
| distance between inner corners | 7.2 | 7.0 | 6.6 | 6.6 | 6.5 | 6.5 | 5.7 | 5.8 | 5.2 | 4.8 | 5.0 | 5.3 | 5.4 |
| Mouth: | | | | | | | | | | | | | |
| width | 7.8 | 7.3 | 7.5 | 7.4 | 6.7 | 6.5 | 7.1 | 5.8 | 5.6 | 6.3 | 5.7 | 6.2 | 6.1 |
| length | 5.9 | 6.7 | 6.3 | 6.1 | 5.1 | 5.3 | 5.4 | 5.0 | 5.0 | 4.0 | 4.5 | 4.9 | 4.8 |
| Labial furrow lengths: | | | | | | | | | | | | | |
| upper | 0.0 | 0.4 | 0.4 | 0.4 | 0.4 | 0.4 | 1.1 | 0.1 | 0.1 | 0.3 | 0.2 | 0.1 | 0.2 |
| lower | 0.8 | 0.9 | 1.4 | 0.6 | 1.1 | 0.9 | 2.8 | 0.7 | 0.6 | 0.4 | 1.0 | 1.1 | 1.1 |
| Gill-opening lengths: | | | | | | | | | | | | | |
| 1st | 3.3 | 3.0 | 3.0 | 2.6 | 2.3 | 2.2 | 2.6 | 2.5 | 2.2 | 1.9 | 1.8 | 2.2 | 2.7 |
| 2nd | 3.3 | 3.2 | 3.3 | 3.0 | 2.7 | 2.5 | 2.8 | 2.9 | 2.6 | 2.2 | 2.1 | 2.1 | 3.2 |
| 3rd | 3.3 | 3.6 | 3.5 | 3.2 | 2.9 | 2.8 | 2.8 | 2.9 | 2.8 | 2.4 | 2.2 | 2.4 | 3.5 |
| 4th | 3.3 | 3.5 | 3.6 | 3.0 | 2.9 | 2.7 | 3.1 | 2.6 | 2.6 | 2.4 | 2.2 | 2.4 | 3.2 |
| 5th | 3.3 | 2.8 | 3.7 | 3.2 | 2.6 | 2.6 | 2.6 | 2.4 | 2.4 | 2.4 | 1.9 | 2.5 | 2.5 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eye: | | | | | | | | | | | | |
| horizontal diameter | 3.3 | 2.7 | 2.4 | 2.5 | 1.8 | 2.0 | 2.0 | 2.0 | 1.6 | 1.6 | 1.4 | 1.4 | 1.5 |
| 1st dorsal fin | | | | | | | | | | | | | |
| length of base | 9.2 | 8.8 | 9.2 | 7.9 | 9.4 | 8.0 | 9.6 | 9.2 | 8.7 | 8.6 | 7.9 | 8.6 | 9.3 |
| posterior margin | – | 3.6 | 4.6 | 3.7 | 4.0 | 4.3 | 4.3 | 4.8 | 5.0 | 3.6 | 4.8 | 4.7 | 4.6 |
| height | 5.9 | 6.3 | 7.5 | 6.1 | 6.5 | 7.0 | 7.7 | 8.7 | 8.3 | 6.9 | 8.6 | 8.1 | 8.9 |
| 2nd dorsal fin: | | | | | | | | | | | | | |
| length of base | 3.5 | 3.3 | 3.4 | 3.5 | 3.2 | 3.4 | 2.6 | 3.2 | 3.0 | 2.8 | 3.4 | 2.6 | 2.8 |
| posterior margin | – | 4.5 | 4.1 | 3.9 | 4.0 | 4.5 | 4.5 | 4.2 | 4.3 | 3.9 | 4.5 | 4.5 | 4.2 |
| height | 2.0 | 1.8 | 1.7 | 1.5 | 1.8 | 2.2 | 2.0 | 1.8 | 1.9 | 1.7 | 1.8 | 2.0 | 1.9 |
| Anal fin: | | | | | | | | | | | | | |
| length of base | 7.8 | 8.4 | 7.0 | 7.9 | 6.9 | 8.0 | 7.1 | 7.4 | 8.0 | 8.2 | 8.4 | 7.4 | 7.2 |
| posterior margin | – | 3.4 | 3.6 | 3.1 | 3.2 | 3.1 | 3.7 | 3.7 | 3.0 | 3.0 | 3.4 | 3.1 | 3.3 |
| height | 2.5 | 2.3 | 2.0 | 1.8 | 2.1 | 2.5 | 3.1 | 2.6 | 2.7 | 2.3 | 2.8 | 2.5 | 3.7 |
| Pectoral fin: | | | | | | | | | | | | | |
| length of base | 5.7 | 5.4 | 5.9 | 6.4 | 6.1 | 6.5 | 6.5 | 6.1 | 6.3 | 5.8 | 5.0 | 5.3 | 5.5 |
| length of anterior margin | 10.0 | 9.1 | 10.1 | 9.6 | 10.5 | 10.8 | 11.1 | 11.6 | 11.1 | 10.0 | 11.1 | 11.6 | 12.4 |
| length of distal margin | 6.5 | 7.0 | 7.5 | 7.0 | 6.9 | 8.4 | 8.2 | 8.2 | 8.3 | 7.8 | 9.0 | 11.0 | 10.2 |
| width | 7.2 | 7.9 | 8.2 | 7.4 | 8.0 | 9.0 | 8.5 | 9.0 | 8.0 | 7.8 | 8.7 | 9.8 | 9.8 |
| Pelvic fin: | | | | | | | | | | | | | |
| length of base | 5.2 | 4.5 | 5.3 | 5.3 | 5.4 | 5.3 | 5.4 | 5.3 | 5.6 | 5.0 | 5.5 | 4.6 | 5.8 |
| length of anterior margin | 5.9 | 4.4 | 5.2 | 4.6 | 5.2 | 5.0 | 5.5 | 5.0 | 5.0 | 5.2 | 4.5 | 4.2 | 5.5 |
| length of distal margin | 3.9 | 4.1 | 4.3 | 3.5 | 3.6 | 4.3 | 4.3 | 4.0 | 5.0 | 4.4 | 5.3 | 5.8 | 5.5 |
| length of claspers | – | 2.4 | 3.5 | – | – | – | 8.5 | 9.8 | – | – | 7.7 | – | – |
| Caudal fin: | | | | | | | | | | | | | |
| length of upper lobe | 22.7 | 23.0 | 21.8 | 22.4 | 22.4 | 22.9 | 23.3 | 23.5 | 20.9 | 23.2 | 20.1 | 22.8 | 22.0 |
| length of lower lobe | 9.3 | 8.5 | 9.2 | 8.3 | 9.3 | 9.6 | 9.4 | 9.5 | 8.7 | 9.3 | 9.4 | 9.1 | 10.0 |
| length from tip to notch | 4.5 | 4.6 | 5.1 | 4.4 | 5.1 | 5.6 | 5.7 | 5.6 | 5.4 | 4.8 | 5.9 | 7.6 | 7.4 |
| notch depth | 5.2 | 4.8 | 4.8 | 5.3 | 4.7 | 5.3 | 4.5 | 5.3 | 4.3 | 4.3 | 4.2 | 3.8 | 4.7 |

[1] Holotype of *Physodon mülleri*.
[2] Lectotype of *Carcharias* (*Scoliodon*) *laticaudus*.

Sexual dimorphism: There is a striking difference in dentition of adult males as compared with females or juvenile males (fig. 3). In adult males the cusps of the teeth are long and slender and the middle and posterior teeth of each side of the lower jaw are erect. The anterior teeth are greatly elongate and flexuous and somewhat round in cross section. Several rows of the anterior lower teeth in the adult male appear to be functional. Sexual dimorphism of dentition in sharks has been reported only for the squalid genus *Deania* (see Bigelow and Schroeder, 1957, and Garrick, 1960). Dental sexual dimorphism also exists in *Rhizoprionodon lalandei*, *R. oligolinx*, and probably *R. taylori*; it also exists to a much lesser degree in *Loxodon*. The phenomenon is probably widespread and unrecognized in sharks. *Physodon* is based on an adult male *S. laticaudus* and the type description of *S. laticaudus* is based on an adult female.

This species is free-living at sizes of at least 126 mm. t.l. (130–150 mm. according to Setna and Sarangdhar, 1949). Maximum size in Indian waters is about 26 inches (approximately 660 mm.). Breeding occurs all year with peak parturition from November through January. Up to 12 embryos occur per uterus, but usually no more than 14 young per female. Mature eggs are small, about one mm. in diameter (Setna and Sarangdhar, 1949).

Thillayampalam (1928) has given a detailed anatomical description of *S. laticaudus* (as *Scoliodon sorrakowa*). Some portions of the work are based on other species (*Rhizoprionodon*), but the study is an important one.

Distribution (see "Material").—This is a common species and its absence from Australia, the Philippines, the Celebes, Moluccas, New Guinea, and Oceania I believe to be real. The distribution seems to indicate that the species is essentially a continentally restricted one, able to traverse only the narrowest passes between coastlines. Setna and Sarangdhar (1949) reported that the species (as *S. sorrakowa*) lived in rocky areas up to three miles offshore in Bombay waters.

Nomenclatural discussion.—As mentioned above, *Physodon mülleri* was based on an adult male of *S. laticaudus*. Its dentition is markedly different from that of the female upon which Müller and Henle's description of *C.* (*S.*) *laticaudus* was based. There are adult males in the syntypic series of *S. laticaudus* but undoubtedly these were not examined for dentition. This is indicated by the fact that, in the first pair of pages 27 and 28 in Müller and Henle's Plagiostomen (see discussion on page 573), the description of *C.* (*S.*) *laticaudus* is of a single stuffed female specimen in the Berlin Museum. In the second pair of pages 27 and 28, additional material (including alcohol-preserved specimens) is listed, but the description is identical with the previous one.

In order to insure the stability of the name *C.* (*S.*) *laticaudus*, I believe that a lectotype should be designated. In the present situation the normal procedure would be to select the single stuffed specimen upon which the original description was based. However, in view of the importance of vertebral characters for shark classification, I have chosen to select one of the alcohol-preserved specimens in the Paris Museum (see "Material").

The type of *C.* (*S.*) *macrorhynchos* Bleeker is missing, but the description and figure are sufficient for placing it in synonymy. Günther (1870) first synonymized Bleeker's species with *S. laticaudus*, and Bleeker, in an unpublished manuscript (*Ennumeratio nova revisa*) in the Leiden museum, accepted this as correct.

There is a history of confusion surrounding the trivial names *sorrakowa* and *palasorra*, both of which have been applied to *S. laticaudus*. Russell (1803), not binomial nomenclature, described "Pala Sorra" and "Sorra Kowah" from Vizgapatam, Coromandel, India. The names used were native common names. Cuvier (1829) added the following in a footnote to the last word under *Le Bleu* (*Sq. glaucus* L.), which is the last species he mentions under *Les Requins:*

> Ajoutez le *Squ. ustus*, Dum. (*Sq. carcharia minor*, Forsk.), Lac., I, VIII, 1; *Requin a nageoires noires*, Quoy et Gaym., Zool. de Freyc., pl. 43, f. 1; le *Sq. glauque*, Lac., I, ix, 1, qui est différent de celui de Bl.; le *Sq. ciliaris*, Schn., pl. 31, dont les cil marquent seulement l'extrême jeunesse, Le *palasorrah* [sic] et le *sorrakowah* [sic], Russ., XIV et un assez grand nombre e'espèce nouvelles que nous décrirons dans notre histoire de poissons.

There is no reason to believe from the information contained above that Cuvier was intending to name Russell's forms. Rather it seems he was merely citing the native names. In support of this is the fact that the generic name (*Sq.*) that appears before the other species is omitted before *palasorrah* and *sorrakowah*. Nevertheless, on the basis of the above quotation most subsequent authors credited Cuvier (1829) with authorship of *Carcharias palasorra* and *C. sorrakowah*. Fowler (1936) first called attention to the fact that the first of these two names could not date from Cuvier (1829) because it was not proposed in binomial form. He did not credit the name, however, nor did he mention *sorrakowah*. Klausewitz (1960) also recognized that *palasorrah* as it appeared in Cuvier (1829) was not a valid name. He assigned authorship of *Carcharias palasorrah* to Bleeker (1853) and placed the name in synonymy with *C. acutus* Rüppell but gave no reasons for his actions. He did not discuss *sorrakowah*.

Müller and Henle (1841), in their monograph of the Plagiostoma, list Russell (1803) in their literature references and mention the "Pana Sorrats" and the "Sorra Kowats" as doubtful synonyms of their

genus *Carcharias*. They make no mention of Cuvier's (1829) treatment of the two forms.

The earliest reference which I can find citing Russell's names in binomial form is Bleeker (1853). Bleeker merely gave a compiled list of species and their Russell equivalents. On page 9 he lists the two as follows:

> Carcharias palasorra Cuv. (spec. dub.) Pala sorrah No. 14
> Carcharias sorrakowa (spec. dub.) Sorra kowah No. 15

On page 80 he lists them as follows:

> Carcharius (?) palasorra Cuv. Pola sorrah Russ. No. 14
> Carcharius (?) sorrah kowah Blkr. Sorrah kowah Russ. No. 15

Bleeker, then, must be recognized as the author of these two names with the species based on Russell (1803).

*Carcharias palasorra* can be recognized from Russell's figure as the same as *Scoliodon laticaudus* and a junior synonym of it. The position of the origin of the pectoral fin beneath the fifth gill-opening places it here. *Carcharias sorrakowa* can be either of two species,

TABLE 5.—*Frequency distribution of precaudal vertebrae number in* Scoliodon laticaudus

| | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| India | 1 | 1 | – | 1 | 3 | 5 | 11 | 8 | 7 | 13 | 5 | 1 | 3 | 1 | – | – |
| Thailand | – | – | – | 1 | 2 | – | – | – | – | – | – | – | – | – | – | – |
| Penang | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – |
| Moluccas | 1 | – | 2 | 3 | – | – | 1 | – | – | – | – | – | – | – | – | – |
| Singapore | – | – | – | 2 | 1 | 1 | 1 | – | – | – | – | – | – | – | – | – |
| Batavia | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| China | – | – | – | – | 1 | – | 2 | 3 | 1 | 2 | 3 | 3 | 1 | 2 | 1 | 1 |
| Japan | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |

*Rhizoprionodon acutus* or *R. oligolinx;* it is doubtful that its exact identity will ever be known. To consider it the same as *R. acutus* is to place it in junior synonymy; to consider it the same as *R. oligolinx* is to give it senior synonymy. This would not be bad were it not for the fact that *C. sorrakowa* almost universally has been considered a senior synonym of the common species *Scoliodon laticaudus*. To recognize the name for a species of *Rhizoprionodon* would be confusing. This is involved further by the fact that the name commonly used for *R. oligolinx* has been *S. palasorra*. Nomenclature can best be served, I think, by recognizing *C. sorrakowa* as a synonym of *R. acutus* and by fixing the name through the designation of a neotype. This I have done in the discussion of *R. acutus* (p. 598).

MATERIAL.—INDIA: ISZZ 7830 (1: ca. 420 mm., dried); Bombay, ANSP 77533 (2: 176–196), MNHM 1123 (1: 518, female, here designated lectotype of *Carcharias* (*Scoliodon*) *laticaudus*), USNM 196135 (1: 542), BMNH 1889.2.1.4151–8 (11: 163–420), NFIS [no number]

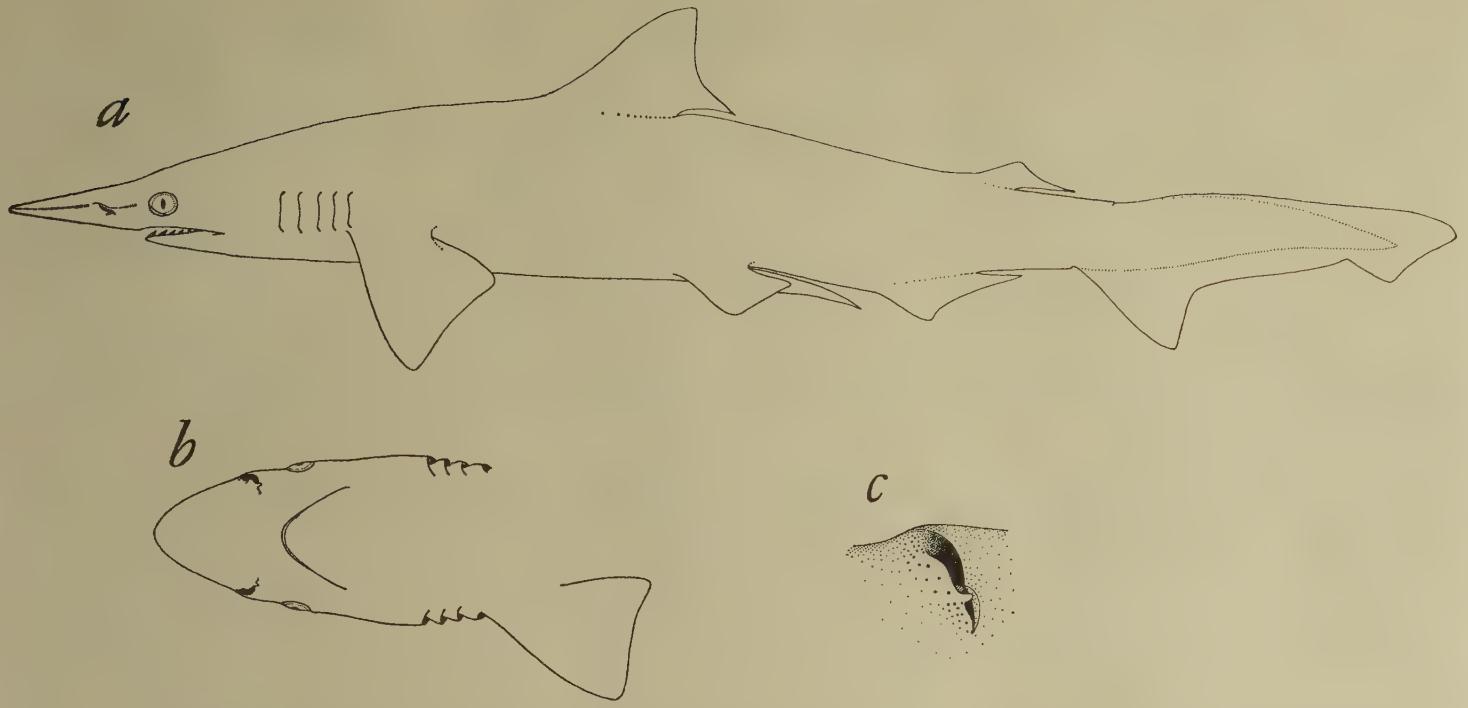


FIGURE 2.—*Scoliodon laticaudus*, SU 38377, 352 mm. t.l., mature male from Singapore: *a*, left side; *b*, underside of head; *c*, enlarged left nostril.

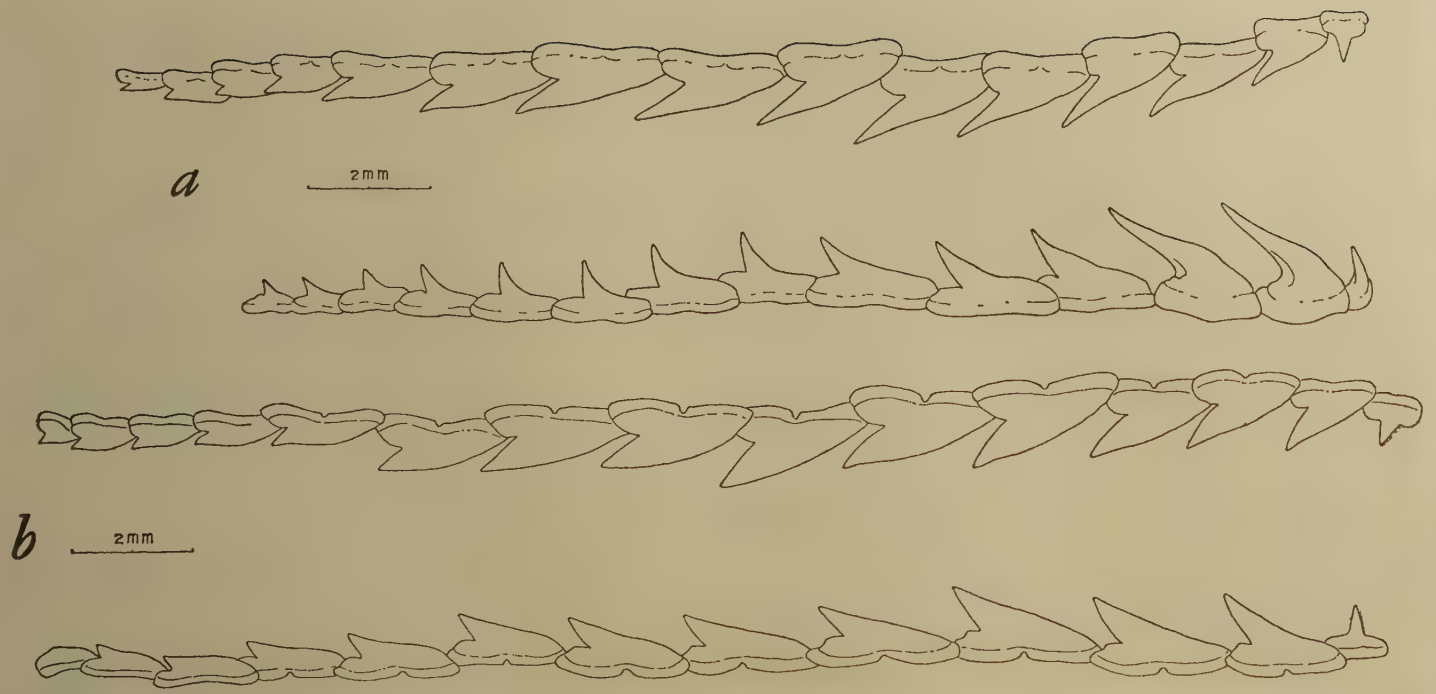


FIGURE 3.—*Scoliodon laticaudus: a*, SU 41982, 378 mm. t.l., mature male from India, right upper and lower teeth (symphysis to the right); *b*, SU 14444, 460 mm. t.l., female from India, right upper and lower teeth (symphysis to the right).

(2: 170–365); Alibag, ZSZM H1391 (3: ca. 167–ca. 281), ZSZM H1374 (1: ca. 402), ZSZM H1375 (8: 264–282), ISH 3/61 (6: 176–506); Kanara, BMNH 1889.2.1.4160 (1: 312); Karwar, ZSZM H1392 (1: 208), ZSZM H1376 (3: 126–218), ISH 4/61 (1: 173); Calicut, BMNH 1899.2.1.4159 (1: 455); Malabar Coast, MNHN 1066 (3: 167–257), MNHN 1122 (1: 423); Pondicherry, UZMK 378 (1: 330); Emur Fisheries Station, Madras Presidency, SU 41983 (1: 207); Madras, BMNH 1889.2.1.4161–3 (2: 337–389); Puri Orissa State, SU 41982 (1: 378); Vizagapatam, SU 1444 (1: 460); Calcutta, SU 41984 (3: 153–165); Bengal, BMNH [no number] (2: 174–240), MNHN 1041 (1: 484, holotype of *Physodon mülleri*); Ceylon, NMV [no number] (1: 175), NMV [no number] (1: 426). GULF OF THAILAND: off Menam River, UZMK [no number] (1: 321); ca. 12°11′ N. and ca. 100°41′ E., GVF 2470 (1: 255). THAILAND: Bangkok, ANSP 60404 (1: 283); Bandon Bight, USNM 86905 (2: 100–137, embryos). MALAYA: Penang, UZMK 377 (1: 370); Singapore, SU 38377 (3: ca. 328–293), MCZ 182 (1: 333), CNHM 15652 (1: 459). JAVA: Batavia, USNM 72479 (1: 422); Straits of Molucca, UZMK 404–409 (6: ca. 210–ca. 253), ANSP 517 (1: 186). EAST INDIAN ARCHIPELAGO: BMNH 1867.11.28.190 (1: 467, female; this specimen is cataloged as holotype of *C.* (*S.*) *macrorhynchos*, but since Bleeker listed only a male, 218 mm., this specimen cannot be a type; the holotype is apparently lost). SARAWAK: BMNH 1895.2.28.74–75, in part (1: ca. 143). CHINA: BMNH 1851.12.27.253–4 (3: 162–245); Chinai, Chusan Island, Tinghai, SU 32434 (4: 258–333); Foochow, USNM 86970 (1: ca. 212), USNM 86334 (1: 228); San-tu, Fukien, ANSP 89616 (1: 323); Wenchow, Chekiang, CAS 875 (1: 275); Amoy, BMNH 1863.2.23.13–16 (4: 159–165), BMNH 1860.7.20.32 (1: 344); Hong Kong, UZMK 376 (1: 581), BMNH 1939.3.23.1 (1: 360), ANSP 76687 (1: 349), SU 13770 (1: ca. 522), SU 13969 (1: 462). JAPAN: BMNH 1862.11.1.30 (1: 155) "TRIESTE" [error]: NMV [no number] (1: 405).

### *Loxodon* Müller and Henle

*Loxodon* Müller and Henle, 1838, Mag. Nat. Hist., new ser., vol. 2, p. 36 (name and diagnosis).

*Loxodon* Müller and Henle, 1838, Arch. Naturg., vol. 4, no. 1, p. 84 (name and diagnosis).

*Loxodon* Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen, p. 61 (type *Loxodon macrorhinus* Müller and Henle, 1841, by monotypy).

DIAGNOSIS.—Sharks of moderate size (reaching at least 905 mm. t.l.) distinguished from other carcharinid genera by the following combination of characters: origin of second dorsal fin ranges from over, and just in advance of, anal axil to slightly behind anal axil (usually); cusps of teeth smooth and obliquely directed rearward; labial furrow on upper jaw poorly developed, usually shorter than

that on lower jaw, which is not visible when the mouth is closed; pectoral fin origin below fourth to third gill-opening; tip of posterior margin of first dorsal fin not reaching beyond level of pelvic origin; distal tip of appressed pectoral fin not reaching much, if any, beyond level of first dorsal origin; hyomandibular pores usually not forming a discrete enlarged series on either side of the corner of the mouth (pores in the series enlarged posteriorly, but gradually, rather than abruptly, as in *Rhizoprionodon*); pores frequently not distinguishable. Other important distinguishing characters as in key couplet 2a (p. 568). (Note: *Loxodon* was described as having a small spiracle. In embryos a tiny spiracle is present, but it is so small that to distinguish it from adjacent pores of the lateral line system is hardly possible. In adults the spiracle is not noticeable to an untrained observer. It is for this reason that *Loxodon* specimens most often have been referred to "*Scoliodon*" species (not *S. laticaudus*). For practical purposes, the spiracle in *Loxodon* is absent. Some specimens of *Scoliodon* and *Rhizoprionodon* have noticeably enlarged pores in the spiracular region. One of these could possibly be the remnant of a spiracle, but I have been unable to demonstrate this.)

The shallow notch in the posterior rim of the orbit is always present though it may not always be obvious to an untrained observer unless compared with the smooth orbital rims of other species (see fig. 4). Occasionally there are two notches or an area around the notch that appears to be scarred. The flap on the nostril is frequently triangular without a developed nipple-like lobe. The labial furrows are very short and, for practical purposes, absent on the upper jaw; however, in one specimen examined, the upper labial furrow on one side was present and comparable to that of some specimens of *Rhizoprionodon*. The distance from the tip of the upper caudal lobe to the subterminal notch is generally much greater and slenderer than in the other species treated in this paper, but sometimes it approaches the size and form as found in *Rhizoprionodon* (figure 4*a* illustrates one such specimen). Both precaudal pits are present but the lower is not as well developed as the upper. The body and fins have a generally slenderer appearance than in *Rhizoprionodon*.

Growth changes: Snout length to origin of pectoral fin, pelvic fin, first dorsal fin, second dorsal fin, anal fin, upper and lower caudal lobes tend, in general, to increase in percent of t.l. with increased t.l.

Eye diameter, length of upper caudal lobe, and distance from tip of upper caudal lobe to notch tend to decrease in percent of t.l. with increased t.l.

From the few specimens examined it does not appear that there is much, if any, change in the relation of the axis of the upper caudal lobe with the horizontal axis of the body with increased t.l.

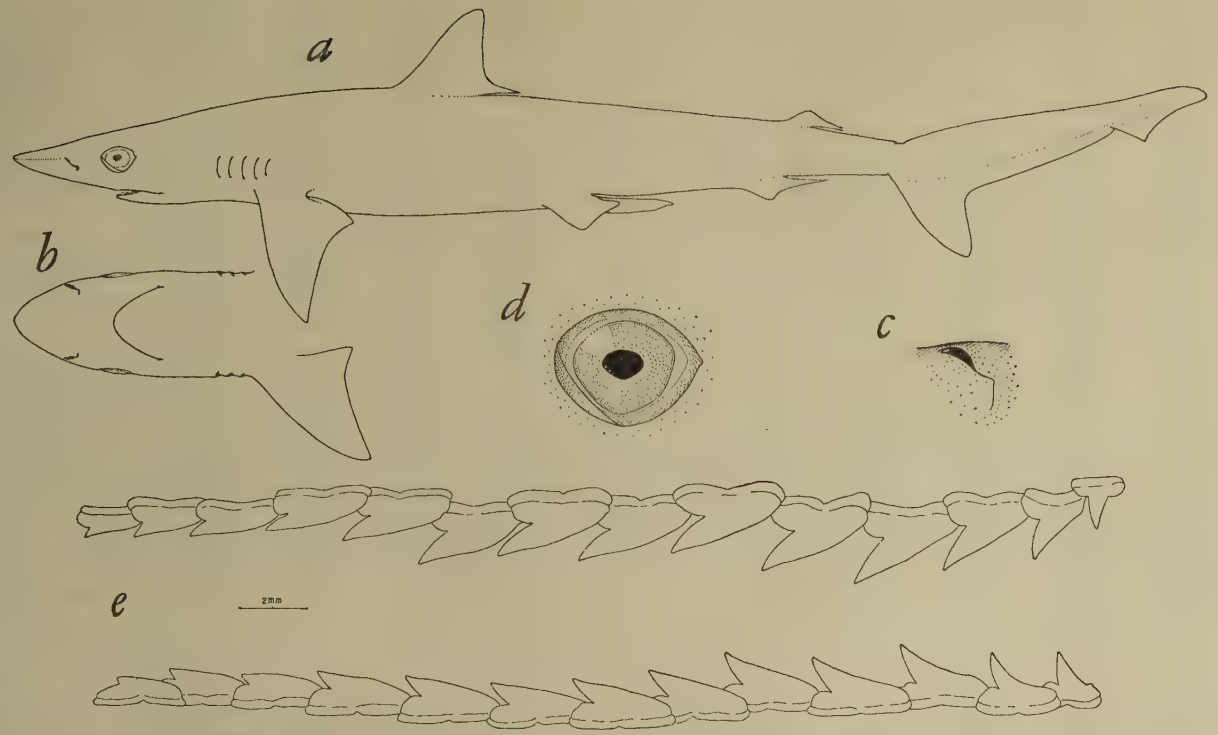


FIGURE 4.—*Loxodon macrorhinus*, USNM 170559, 745 mm. t.l., mature male from the Philippine Islands: *a*, left side (note double notch on posterior rim of orbit); *b*, underside of head; *c*, enlarged left nostril; *d*, USNM 197349, 544 mm. t.l., immature male from the Philippine Islands, enlarged left eye (note single notch on posterior rim of orbit); *e*, UMMZ 177117, 668 mm. t.l., female from the East China Sea, right upper and lower teeth (symphysis to the right; base line refers only to teeth).

TABLE 6.—*Proportional dimensions in percent of total length of* Loxodon macrorhinus

| | ♂ 356 mm. Embryo Philippines SU 26821 | ♂ 391 mm. Embryo Philippines SU 26819 | ♀ 421 mm. Embryo Mauritius MCZ 513 | ♂ 498 mm. Philippines SU 13670 | ♂ 513 mm. Amboina BMNH 1858.4.21.511 | ♂ 521 mm. Queensland QMB I13/1526 [1] | ♀ 543 mm. Amboina RNH 7371 | ♀ 572 mm. Philippines USNM 170560 | ♂ 573 mm. Amboina BMNH 1867.11.28.-174 | ♂ 660 mm. Misol BMNH 1870.8.31.70 | ♀ 668 mm. East China Sea UMMZ 177117 | ♂ 745 mm. Philippines USNM 170559 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | | | |
| outer nostrils | 3.8 | 3.8 | 4.0 | 4.6 | 4.7 | 5.4 | 4.7 | 4.5 | 4.5 | 4.9 | 4.5 | 4.2 |
| eye | 7.1 | 7.0 | 7.1 | 7.6 | 7.8 | 8.9 | 7.8 | 8.0 | 7.9 | 8.4 | 8.1 | 7.2 |
| mouth | 8.4 | 8.4 | 8.6 | 9.0 | 8.7 | 9.8 | 8.8 | 9.1 | 8.7 | 9.4 | 9.0 | 8.3 |
| 1st gill-opening | 17.1 | 16.4 | 16.1 | 15.9 | 15.9 | 18.2 | 16.0 | 16.1 | 16.4 | 15.9 | 17.1 | 17.0 |
| pectoral origin | 19.9 | 19.7 | 19.0 | 19.3 | 19.5 | 21.2 | 19.0 | 19.4 | 19.6 | 18.9 | 20.2 | 20.0 |
| pelvic origin | 40.2 | 38.9 | 42.0 | 41.8 | 42.8 | 44.0 | 42.2 | 42.7 | 43.3 | 42.1 | 45.2 | 44.4 |
| 1st dorsal origin | 29.2 | 29.4 | 30.9 | 30.3 | 31.3 | 32.6 | 28.5 | 30.6 | 30.6 | 30.0 | 33.5 | 31.8 |
| 2nd dorsal origin | 60.2 | 57.6 | 60.6 | 61.3 | 61.6 | 61.8 | 59.8 | 61.4 | 62.8 | 61.6 | 64.3 | 65.1 |
| anal fin origin | 53.0 | 53.7 | 56.3 | 56.8 | 57.5 | 58.7 | 56.6 | 58.3 | 55.3 | 57.6 | 60.4 | 61.0 |
| upper caudal origin | 71.0 | 68.4 | 71.6 | 71.7 | 71.6 | 73.0 | 70.3 | 73.0 | 73.5 | 72.3 | 74.9 | 75.0 |
| lower caudal origin | 69.0 | 67.0 | 69.8 | 70.7 | 70.4 | 71.7 | 69.0 | 72.6 | 71.8 | 71.1 | 73.5 | 73.8 |
| Nostrils: | | | | | | | | | | | | |
| distance between inner corners | 5.2 | 4.9 | 5.5 | 5.2 | 5.1 | 5.8 | 4.6 | 4.5 | 4.7 | 5.3 | 5.1 | 5.2 |
| Mouth: | | | | | | | | | | | | |
| width | 4.9 | 4.9 | 5.2 | 5.6 | 5.4 | 5.7 | 5.6 | 5.1 | 5.2 | 5.4 | 5.4 | 5.9 |
| length | 4.0 | 4.1 | 3.8 | 3.4 | 3.9 | 3.5 | 3.7 | 4.0 | 3.8 | 3.1 | 4.2 | 3.7 |
| Labial furrow lengths: | | | | | | | | | | | | |
| upper | 0.2 | 0.4 | – | 0.3 | 0.2 | – | 0.2 | 0.1 | 0.3 | 0.2 | 0.3 | 0.2 |
| lower | 0.8 | 0.8 | – | 1.1 | 0.8 | – | 0.8 | 0.9 | 1.0 | 0.6 | 0.8 | 0.9 |
| Gill-opening lengths: | | | | | | | | | | | | |
| 1st | 1.7 | 1.7 | 1.8 | 1.6 | 1.6 | 1.8 | 1.4 | 1.4 | 1.6 | 1.5 | 1.9 | 1.6 |
| 2nd | 1.7 | 1.7 | 1.8 | 1.6 | 1.9 | 2.1 | 1.6 | 1.6 | 1.7 | 1.8 | 1.9 | 1.6 |
| 3rd | 1.7 | 1.7 | 1.9 | 1.8 | 1.9 | 2.3 | 1.7 | 1.6 | 1.7 | 1.9 | 2.1 | 1.9 |
| 4th | 1.6 | 1.6 | 1.9 | 1.8 | 1.8 | 2.2 | 1.7 | 1.6 | 1.8 | 2.0 | 2.0 | 1.9 |
| 5th | 1.4 | 1.5 | 1.7 | 1.4 | 1.7 | 1.7 | 1.4 | 1.2 | 1.4 | 1.4 | 1.4 | 1.3 |
| Eye: | | | | | | | | | | | | |
| horizontal diameter | 3.6 | 3.6 | 3.3 | 3.0 | 3.0 | 2.9 | 2.8 | 2.8 | 2.6 | 2.6 | 2.6 | 2.8 |
| 1st dorsal fin: | | | | | | | | | | | | |
| length of base | 7.6 | 6.9 | 6.6 | 6.8 | 6.5 | 7.1 | 7.3 | 6.3 | 6.8 | 7.0 | 7.5 | 7.2 |
| posterior margin | 3.4 | 3.3 | 3.3 | 3.8 | 3.3 | 3.8 | 3.5 | 3.5 | 3.6 | 3.8 | 3.7 | 3.9 |
| height | 6.2 | 5.6 | 6.9 | 7.9 | 7.6 | 7.6 | 7.5 | 7.9 | 7.5 | 8.1 | 7.3 | 7.2 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2nd dorsal fin: | | | | | | | | | | | | |
| length of base | 2.0 | 2.2 | 1.8 | 2.1 | 2.0 | 2.0 | 2.2 | 2.4 | 1.9 | 2.0 | 2.2 | 2.1 |
| posterior margin | 4.2 | 4.1 | 4.8 | 4.6 | 4.3 | 4.8 | 4.2 | 4.5 | 4.4 | 4.4 | 4.9 | – |
| height | 1.3 | 1.3 | 1.4 | 1.2 | 1.5 | 1.5 | 1.5 | 1.2 | 1.6 | 1.5 | 1.5 | 1.1 |
| Anal fin: | | | | | | | | | | | | |
| length of base | 4.2 | 3.8 | 4.2 | 3.8 | 3.3 | 3.8 | 3.8 | 4.1 | 3.6 | 4.0 | 3.7 | 3.9 |
| posterior margin | 3.9 | 3.8 | 3.3 | 4.2 | 3.7 | 4.1 | 3.7 | 4.0 | 3.7 | 3.9 | 4.5 | 3.8 |
| height | 1.7 | 1.8 | 1.5 | 1.5 | 1.9 | 1.9 | 1.8 | 1.6 | 2.1 | 2.0 | 2.3 | 1.5 |
| Pectoral fin: | | | | | | | | | | | | |
| length of base | 4.2 | 4.4 | 4.0 | 4.1 | 3.9 | 4.3 | 4.1 | 4.2 | 4.0 | 4.1 | 4.8 | 4.6 |
| length of anterior margin | 11.5 | 11.5 | 11.9 | 11.5 | 11.7 | 12.5 | 11.4 | 11.4 | 11.3 | 11.8 | 12.7 | 11.7 |
| length of distal margin | 9.0 | 7.9 | 7.6 | 8.2 | 8.4 | 8.9 | 8.2 | 8.6 | 8.5 | 9.2 | 8.8 | 9.5 |
| width | 7.6 | 7.2 | 6.9 | 7.2 | 6.6 | 7.9 | 6.5 | 7.0 | 6.8 | 7.0 | 7.5 | 7.8 |
| Pelvic fin: | | | | | | | | | | | | |
| length of base | 3.7 | 3.7 | 3.1 | 3.8 | 3.3 | 3.6 | 3.6 | 4.0 | 3.5 | 3.6 | 3.7 | 4.0 |
| length of anterior margin | 4.7 | 4.4 | 4.8 | 4.4 | 3.9 | 3.8 | 3.6 | 4.0 | 4.2 | 3.9 | 4.6 | 3.7 |
| length of distal margin | 4.0 | 3.5 | 3.6 | 3.4 | 3.3 | 3.8 | 3.9 | 3.5 | 3.8 | 3.9 | 4.2 | 3.7 |
| length of claspers | 2.6 | 2.4 | – | 2.3 | 2.3 | 2.7 | – | – | 2.8 | 2.4 | – | 7.2 |
| Caudal fin: | | | | | | | | | | | | |
| length of upper lobe | 29.5 | 31.7 | 29.0 | 28.5 | 28.3 | 27.0 | 29.7 | 29.0 | 27.0 | 27.4 | 25.0 | 26.0 |
| length of lower lobe | 9.8 | 9.8 | 10.4 | 8.8 | 10.2 | 9.2 | 10.0 | – | 9.2 | 9.3 | 9.4 | 9.5 |
| length from tip to notch | 8.0 | 8.2 | 7.1 | 7.7 | 8.0 | 7.1 | 6.8 | 7.2 | 7.6 | 6.7 | 6.0 | 6.2 |
| notch depth | 3.5 | 2.8 | 3.1 | 3.0 | 3.3 | 3.6 | 2.7 | 3.0 | 2.6 | 3.0 | 3.0 | 3.0 |

[1] Holotype of *Scoliodon affinis*.

TABLE 7.—*Frequency distribution of precaudal vertebrae number of* Loxodon macrorhinus

| | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Holotype (locality unknown) | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Mauritius | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Red Sea | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Gulf of Oman | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Sumatra | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Amboina and Misol | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 2 | 1 | 1 |
| Philippine Islands | – | – | – | – | – | – | 2 | 1 | 1 | 1 | 3 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Formosa | – | 1 | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| East China Sea | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Australia | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – |

This genus is at least superficially closest to *Rhizoprionodon*.

A single species distributed from the southwest coast of Africa to the Red Sea, India, the Philippines, Dutch East Indies, and Australia.

### *Loxodon macrorhinus* Müller and Henle

FIGURE 4; PLATE 1A

*Loxodon macrorhinus* Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen, p. 61, pl. 25 (embryo, locality unknown).

*Carcharias (Scoliodon) dumerili* Bleeker, 1856, Act. Soc. Sci. Indo-Neerl., vol. 1, p. 70 (Amboina).

*Scoliodon jordani* Ogilby, 1908, Proc. Roy. Soc. Queensland, vol. 21, p. 88 (outer Caloundra Bank, Queensland).

*Scoliodon affinis* Ogilby, 1912, Mem. Queensland Mus., vol. 1, p. 29 (Noosa Head, south Queensland).

*Scoliodon ceylonensis* Setna and Sarangdhar, 1946, Proc. Nat. Inst. Sci. India, vol. 12, no. 5, p. 252 (Bombay waters; no type material listed).

DIAGNOSIS.—Distinctive characters are those of the genus (q.v.).

DESCRIPTION (see also table 6).—Precaudal vertebrae 77–106 (table 7), centra in posterior monospondylous region elongate (plate 1A); caudal vertebrae 71–86; total vertebrae 148–191; upper teeth 12–1–12 to 13–1–14; lower teeth 12–12 to 14–14 (higher, or lower, counts in upper and lower jaws correlated).

Denticles imbricate, 3- to 5-ridged and 3- to 4-toothed.

Color of preserved specimens: brown to gray brown above, pale below. Pectoral and pelvic fins pale-edged; caudal either pale-edged or with a narrow black margin; first dorsal dusky distally. The distal portions of the claspers of adult males paler than remainder.

A low, short interdorsal ridge is sometimes present close to the first dorsal fin (e.g., one specimen from the Philippines had it, another did not).

The largest immature male seen, from Misol Island, was 660 mm. t.l., and had a clasper length equal to 2.4 percent of the t.l. The smallest mature male, from the Philippines, was 745 mm. t.l. and had a clasper length equal to 7.2 percent of the t.l. The skin of a male approximately 900 mm. t.l. from Kenya, Africa, had a clasper length of 63.5 mm., ca. 7.3 percent of t.l.

The largest embryo seen was 421 mm. t.l. and the smallest non-embryo specimen was 429 mm. t.l.

The cusps of the teeth of adult males may be slightly more erect than those of females, but the difference is not striking. The cusps are smooth, even in large specimens.

DISTRIBUTION (see "Material").—The presence of this species in India is based on Setna and Sarangdhar (1950, as *Scoliodon acutus*).

Its apparent absence from Oceania is in accord with the distributions of the other species discussed in the present study.

The species is quite common in Philippine waters. I saw large numbers of small specimens in the Manila fish market during April 1962. Its relative abundance elsewhere is unknown although Setna and Sarangdhar (1950) report it as uncommon in Indian waters.

Wheeler (1959), who gave an excellent description of *Loxodon*, reported the species common at Zanzibar. His longest specimen was 905 mm. An 850 mm. female contained two embryos. One specimen was caught in a trammel net at a depth of about four fathoms.

NOMENCLATURAL DISCUSSION.—The types of the nominal forms, except *Scoliodon ceylonensis* Setna and Sarangdhar and *S. jordani* Ogilby, were examined and apparently are the same species. The holotype of *S. jordani* was reported by Ogilby (1916) as having been destroyed. The short outward-directed upper labial groove and the appressed pectorals extending only to beneath the origin of the first dorsal fin of *S. jordani* indicate that it was probably a *Loxodon*. No type was designated for *S. ceylonensis* but the tooth counts and the nature of the labial folds as given in the original description place it in *Loxodon*. Setna and Sarangdhar (1950), without comment, placed their species in synonymy with *Carcharias acutus* Rüppell; however, the figures and description they give are clearly those of a *Loxodon*, and, as such, confirm my suspicions concerning the original description.

MATERIAL.—NO LOCALITY: ISZZ 4479 (1: ca. 315 mm., embryo, holotype of *Loxodon macrorhinus*). KENYA: Shimoni, DIRU 15A (1: ca. 900, head and skin). MAURITIUS ISLAND: MCZ 513 (1: 421, embryo). SEYCHELLES ISLANDS: BMNH 1869.5.14.15 (2: ca. 315–ca. 335, embryos). RED SEA: NFIS 926 (1: ca. 345, embryo), NMV [no number] (1: 858). EGYPT: Kosseir, SMNS 1787 (1: ca. 375, embryo). GULF OF OMAN: Muscat, BMNH 1892.1.16.9–10 (1: 734). SUMATRA: Padang, NMV [no number] (1: 691). MISOL ISLAND: BMNH 1870.8.31.70 (or .79?) (1: 660). AMBOINA ISLAND: BMNH 1858.4.21.511 (1: 513), BMNH 1867.11 28.174 (1: 573, male, listed as type of *Carcharias dumerili* Bleeker, but Bleeker described the species from a 553 mm. female), RNH 7371 (1: 543, holotype of *Carcharias dumerili*). AUSTRALIA: Queensland, QMB [number missing] (1: 797, this specimen was with a group of sharks, all from Queensland; tags had corroded); Noosa Head, QMB I13/1526 (1: 521, holotype of *Scoliodon affinis*). PHILIPPINE ISLANDS: Oriental Negros, Dumaguete, SU 26821 (1: 356, embryo), SU 26819 (1: 391, embryo), SU 13670 (1: 498); Limbones Cove, USNM 170560 (1: 572); off Luzon Point (1: 745); Manila area, USNM 197349 (3: 500–544). FORMOSA: Thape, ISZZ 6964 (2: 429–443). JAPAN: East China Sea, UMMZ 177117 (1: 668).

### *Rhizoprionodon* Whitley

*Rhizoprion* Ogilby, 1915, Mem. Queensland Mus., vol. 3, p. 132 (type *Carcharias* (*Scoliodon*) *crenidens* Klunzinger, 1880, a synonym of *Carcharias acutus* Rüppell, 1835, by original designation), a junior homonym of *Rhizoprion* Jourdan, 1861, a fossil Cetacean.

*Rhizoprionodon* Whitley, 1929, Australian Zool., vol. 5, p. 354 (a substitute name for *Rhizoprion* Ogilby).

*Protozygaena* Whitley, 1940, The fishes of Australia, vol. 1, p. 110 (type *Physodon taylori* Ogilby, 1915, by original designation; retained in my study as a subgenus).

DIAGNOSIS.—Sharks of small to moderate size (reaching a t.l. of at least 1000 mm.) distinguished from other carcharhinid genera by the following combination of characters: origin of second dorsal fin ranges from over middle of anal base (rarely) to over anal axil; cusps of teeth smooth to serrulate and obliquely directed rearward; labial furrow on upper jaw usually well developed, except in most specimens of *R. oligolinx* and *R. taylori;* lower labial furrow visible when mouth is closed; pectoral fin origin below fourth to third gill-opening; tip of posterior margin of first dorsal fin not reaching much, if any, beyond level of pelvic origin; distal tip of appressed pectoral fin not extending posteriorly much, if any, past level of anterior two-thirds of first dorsal base; differing from all carcharhinids I have examined in having a discrete series (sometimes irregularly biserial) of enlarged hyomandibular pores on the outer side of each corner of the mouth. Other distinguishing characters as in key couplets 1b and 2b (p. 568).

SUBGENERA.—I recognize two subgenera, *Rhizoprionodon* and *Protozygaena*, within the genus. The nominal subgenus includes *R. terraenovae*, *R. porosus*, *R. acutus*, and *R. longurio;* the subgenus *Protozygaena* includes *R. lalandei*, *R. taylori*, and *R. oligolinx*.

The nominal subgenus differs from *Protozygaena* in having markedly elongate centra in the posterior monospondylous region (plate 2A), as opposed to scarcely elongate centra in that region (plate 2B, C); in only rarely having more precaudal vertebrae than caudal vertebrae, as opposed to always having more precaudal than caudal vertebrae in *Protozygaena;* in the absence of a marked sexual dimorphism of the dentition of the lower jaw of adults, as opposed to its presence in *Protozygaena;* in having the cusps of at least some teeth noticeably serrulate in large specimens, as opposed to smooth or faintly irregular cusps in *Protozygaena;* in generally having more teeth, a longer upper labial furrow, in attaining a size of 900–1000 mm., and in having males mature only at sizes greater than 600 mm., as opposed to fewer teeth, a shorter upper labial furrow, in attaining a size of less than 700 mm., and in having males mature at less than 600 mm. (as small as 380 mm. in *R. oligolinx*).

TABLE 8.—*Frequency distribution of total number of enlarged hyomandibular pores on both sides of head in* Rhizoprionodon

| | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *R. longurio* | – | – | – | – | – | – | – | – | – | 1 | 3 | 2 | 5 | 3 | 2 | 10 | 1 | 1 | 2 | 1 | 1 | 1 | – | – | – | – | – | – | – | – | – | – |
| *R. acutus* | – | – | – | – | – | – | – | – | 1 | 7 | 8 | 11 | 8 | 17 | 10 | 17 | 10 | 8 | 10 | 4 | 2 | 1 | 4 | – | – | – | – | – | – | – | – | – |
| *R. terraenovae* | – | – | – | – | – | – | – | – | – | 1 | – | 3 | 4 | 2 | 5 | 3 | 4 | 3 | 5 | 8 | 3 | 6 | 3 | 1 | – | 1 | – | 1 | – | – | – | – |
| *R. porosus* | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 2 | 2 | 2 | 2 | 4 | 6 | 1 | 4 | 2 | 1 | 1 | 1 | – | – | – | – | – | – | 1 |
| *R. lalandei* | – | – | – | – | – | – | – | 1 | – | – | 1 | 1 | 1 | 5 | 9 | 3 | 1 | – | 3 | 1 | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. oligolinx* | 2 | 3 | 2 | 11 | 6 | 8 | 12 | 10 | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *R. taylori* | – | – | – | – | – | – | – | – | 1 | 1 | 3 | – | – | – | 2 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |

TABLE 9.—*Frequency distribution of precaudal vertebrae number of* Rhizoprionodon acutus

| | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Madeira Islands | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – |
| Africa | | | | | | | | | | | | | | | | | | | | | | | | | |
| West Coast | – | – | – | – | – | – | – | – | – | 1 | 2 | 1 | – | – | 2 | – | 2 | 1 | – | – | 1 | – | – | – | – |
| East Coast | – | – | – | – | – | – | – | – | – | – | – | – | 4 | 6 | 5 | 2 | 2 | – | – | – | – | – | – | – | – |
| Madagascar | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – |
| Red Sea | – | – | – | – | – | – | 1 | – | – | – | 1 | – | 2 | 1 | 1 | 2 | 2 | 1 | – | – | – | – | – | – | – |
| Gulf of Oman | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – |
| Persian Gulf | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 2 | 2 | – | 1 | – | – | – | – | – | – | – |
| India and Ceylon | – | – | 1 | – | 4 | 1 | – | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Andaman Islands | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – |
| Thailand | – | – | 1 | 1 | – | – | 2 | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Singapore-Bintang | – | – | – | 1 | – | 1 | – | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Padang, Sumatra | – | – | – | – | – | 2 | 1 | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Batjan and Macassar | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | 1 |
| Aru Islands | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – |
| Australia | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 | 3 | 5 | 2 | – | 1 | – | 1 | – | – | – |
| Sitankai, Philippines | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | – |
| Sarawak-North Borneo | – | – | – | – | 1 | 1 | 1 | 1 | – | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Mindanao, Philippines | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Panay, Philippines | – | – | – | – | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Unisan, Philippines | – | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Luzon, Philippines | 2 | 2 | 8 | 8 | 3 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Formosa | – | – | – | – | 1 | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Japan | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |

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TABLE 10.—*Proportional dimensions in percent of total length of* Rhizoprionodon acutus

| | ♂ 368 mm. India SU 30502 [1] | ♀ 387 mm. Liberia USNM 179719 | ♂ 442 mm. Red Sea NFIS 761 | ♂ 445 mm. Red Sea HU E57/666 | ♂ 455 mm. Queensland QMB 12/292 [2] | ♀ 477 mm. Nigeria BMNH 1936.8.20.1 | ♂ 500 mm. Northern Territory USNM 174076 | ♀ 553 mm. Red Sea USNM 47603 | ♂ 568 mm. Persian Gulf USNM 148103 | ♂ 624 mm. Red Sea HUI E57/664 | ♂ 678 mm. Liberia USNM 179718 | ♂ 678 mm. Red Sea HUI E57/663 | ♀ 690 mm. Persian Gulf USNM 148104 | ♀ 785 mm. Northern Territory USNM 174077 | ♂ 800 mm. Queensland USNM 176744 | ♀ 817 mm. Zanzibar MCZ 401 [3] | ♀ 820 mm. Formosa USNM 191192 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | | | | | | | | |
| outer nostrils | 5.4 | 5.1 | 4.7 | 5.2 | 4.7 | 4.7 | 4.6 | 5.4 | 4.7 | 5.0 | 4.6 | 4.3 | 4.7 | 4.2 | 4.7 | 4.8 | 4.8 |
| eye | 8.7 | 8.8 | 7.9 | 8.5 | 8.2 | 8.0 | 8.0 | 8.3 | 7.7 | 8.4 | 7.8 | 7.2 | 7.8 | 7.1 | 7.6 | 8.0 | 7.6 |
| mouth | 9.5 | 9.8 | 8.8 | 9.3 | – | 8.8 | 9.0 | 8.7 | 8.3 | 8.8 | 8.7 | 8.0 | 8.8 | 7.9 | 8.3 | 8.2 | 8.2 |
| 1st gill opening | – | 18.9 | 19.0 | 19.8 | 18.2 | 19.5 | 18.6 | 18.1 | 19.2 | 19.6 | 18.1 | 19.3 | 18.9 | 17.8 | 18.9 | 17.7 | 18.0 |
| pectoral origin | 22.3 | 22.5 | 22.4 | 22.5 | 21.1 | 22.4 | 21.6 | 21.2 | 21.5 | 22.3 | 21.4 | 22.1 | 21.8 | 20.5 | 22.1 | 20.4 | 20.7 |
| pelvic origin | 45.4 | 45.8 | 44.1 | 45.0 | 42.6 | 46.2 | 43.8 | 45.8 | 44.6 | 44.9 | 44.0 | 46.2 | 49.0 | 44.6 | 46.2 | 47.6 | 45.4 |
| 1st dorsal origin | 31.0 | 30.0 | 28.7 | 29.7 | 29.2 | 30.6 | 29.0 | 30.8 | 29.6 | 29.2 | 29.9 | 29.8 | 30.8 | 28.7 | 30.5 | 30.2 | 31.1 |
| 2nd dorsal origin | 62.7 | 62.2 | 60.8 | 61.4 | 61.7 | 64.2 | 63.0 | 63.4 | 63.6 | 62.5 | 63.2 | 64.4 | 67.0 | 65.0 | 66.5 | 65.6 | 65.6 |
| anal fin origin | 60.4 | 58.9 | 58.4 | 58.0 | 57.6 | 60.0 | 58.4 | 59.8 | 59.5 | 59.4 | 59.2 | 61.2 | 63.9 | 60.2 | 62.2 | 62.2 | 61.8 |
| upper caudal origin | 73.4 | 73.2 | 76.6 | 72.4 | 73.8 | 74.8 | 74.0 | 76.3 | 72.8 | 73.6 | 73.8 | 76.7 | 77.0 | 76.2 | 75.2 | 75.5 | 75.6 |
| lower caudal origin | 72.2 | 71.8 | 71.0 | 70.8 | 71.8 | 73.2 | 72.0 | 72.0 | 71.3 | 72.1 | 73.0 | 75.0 | 75.5 | 74.2 | 74.4 | 74.7 | 74.4 |
| Nostrils: | | | | | | | | | | | | | | | | | |
| distance between inner corners | 5.4 | 5.6 | 4.9 | 5.0 | 4.9 | 5.6 | 5.1 | 4.9 | 5.1 | 4.9 | 4.9 | 4.8 | 5.1 | 4.7 | 5.1 | 4.7 | 4.6 |
| Mouth: | | | | | | | | | | | | | | | | | |
| width | 6.5 | 7.7 | 7.0 | 6.5 | 6.9 | 7.1 | 6.9 | 6.3 | 7.1 | 6.2 | 6.7 | 6.8 | 7.3 | 7.0 | 6.8 | 7.3 | 6.4 |
| length | 5.2 | 4.4 | 4.5 | 4.5 | 4.1 | 4.9 | 4.4 | 4.3 | 4.1 | 4.4 | 4.4 | 4.4 | 4.6 | 4.5 | 4.5 | 4.9 | 4.6 |
| Labial furrow lengths: | | | | | | | | | | | | | | | | | |
| upper | 1.8 | 1.8 | 1.4 | 2.0 | 1.9 | 1.8 | 2.0 | 1.6 | 1.8 | 1.6 | 1.7 | 1.8 | 1.6 | 1.9 | – | 1.8 | 1.7 |
| lower | 1.2 | 1.4 | 1.4 | 1.0 | 1.3 | 1.4 | 1.2 | 1.3 | 1.4 | 1.5 | 1.3 | 1.2 | 1.5 | 1.5 | – | 1.3 | 1.7 |
| Gill-opening lengths: | | | | | | | | | | | | | | | | | |
| 1st | – | 1.9 | 1.9 | 1.9 | 1.7 | 1.7 | 1.7 | 1.4 | 1.8 | 1.8 | 1.8 | 2.1 | 2.1 | 1.8 | 1.5 | 1.9 | 1.8 |
| 2nd | 2.0 | 2.1 | 2.0 | 2.2 | 2.0 | 2.0 | 2.2 | 1.8 | 2.1 | 2.1 | 2.1 | 2.4 | 2.5 | 2.1 | 1.9 | 2.1 | 2.0 |
| 3rd | 2.3 | 2.2 | 2.0 | 2.4 | 2.3 | 2.2 | 2.4 | 2.0 | 2.6 | 2.3 | 2.1 | 2.8 | 2.6 | 2.3 | 2.1 | 2.5 | 2.1 |
| 4th | 2.4 | 2.0 | 2.0 | 2.2 | 2.4 | 2.2 | 2.3 | 2.0 | 2.8 | 2.2 | 2.1 | 2.6 | 2.6 | 2.2 | 2.2 | 2.4 | 2.0 |
| 5th | 2.0 | 1.6 | 1.6 | 1.6 | 1.9 | 1.8 | 1.8 | 1.4 | 2.3 | 1.8 | 1.6 | 1.9 | 2.1 | 1.8 | 1.6 | 1.9 | 1.6 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eye: | | | | | | | | | | | | | | | | |
| horizontal diameter | 3.0 | 2.7 | 2.4 | 2.4 | 2.5 | 2.7 | 2.3 | 2.5 | 2.3 | 2.3 | 2.1 | 2.2 | 2.3 | 1.9 | 2.2 | 2.1 | 2.2 |
| 1st dorsal fin: | | | | | | | | | | | | | | | | | |
| length of base | 9.8 | 8.9 | 9.4 | 8.9 | 9.3 | 8.7 | 9.4 | 8.9 | 9.8 | 9.2 | 9.0 | 9.7 | 9.8 | 10.1 | 9.4 | 9.6 | 8.9 |
| posterior margin | 4.9 | 4.6 | 4.8 | 4.7 | 4.5 | 5.1 | 4.5 | 4.5 | 4.7 | 4.6 | 4.9 | 4.4 | 4.8 | 4.2 | 4.4 | 5.1 | 4.9 |
| height | 9.2 | 8.7 | 9.5 | – | 8.5 | 8.8 | 8.6 | 8.7 | 9.2 | 9.5 | – | – | 8.6 | 8.2 | – | 9.6 | 8.1 |
| 2nd dorsal fin: | | | | | | | | | | | | | | | | | |
| length of base | 3.0 | 3.0 | 2.9 | 2.5 | 3.2 | 2.7 | 2.5 | 2.5 | 3.1 | 2.9 | 2.8 | 3.1 | 2.4 | 2.5 | 2.3 | 2.5 | 2.3 |
| posterior margin | 4.6 | 4.6 | 5.3 | 5.0 | 4.5 | 5.1 | 4.7 | 4.9 | 4.7 | 5.0 | 4.9 | 4.5 | 5.1 | 4.3 | 4.5 | 5.2 | 5.0 |
| height | 2.2 | 2.0 | 1.8 | – | 1.8 | 2.2 | 1.9 | 1.8 | 2.1 | 2.0 | 1.9 | 1.9 | 1.9 | – | 1.6 | 2.1 | 1.8 |
| Anal fin: | | | | | | | | | | | | | | | | | |
| length of base | 5.4 | 4.8 | 4.4 | 4.9 | 5.2 | 5.1 | 4.9 | 4.5 | 5.3 | 5.2 | 4.9 | 5.3 | 4.8 | 4.8 | 4.5 | 4.6 | 4.6 |
| posterior margin | 4.4 | 4.4 | 4.8 | 4.4 | 4.1 | 4.6 | 4.3 | 4.3 | 4.5 | 4.6 | 4.6 | 4.4 | 4.1 | 4.3 | 4.2 | 4.7 | 4.6 |
| height | 3.5 | 3.4 | 2.8 | 2.5 | 2.5 | 3.2 | 2.8 | 2.2 | 2.8 | 2.9 | 2.9 | 2.4 | 2.7 | 2.9 | 2.8 | 3.3 | 2.5 |
| Pectoral fin: | | | | | | | | | | | | | | | | | |
| length of base | 5.4 | 5.0 | 4.7 | 5.1 | 4.6 | 5.2 | 5.3 | 5.8 | 5.4 | 5.3 | 5.2 | 5.0 | 5.7 | 5.4 | 5.5 | 5.2 | 5.3 |
| length of anterior margin | 13.3 | 12.9 | 12.7 | 12.6 | 11.8 | 13.7 | 12.8 | 13.0 | 13.6 | 13.6 | 13.0 | 13.1 | 13.6 | 13.1 | 12.9 | 14.1 | 13.1 |
| length of distal margin | 8.7 | 8.5 | 9.3 | 9.6 | 8.5 | 10.6 | 9.4 | 9.3 | 10.0 | 9.9 | 10.0 | 9.9 | 10.5 | 9.9 | 10.2 | 11.2 | 9.8 |
| width | 7.6 | 8.2 | 7.6 | 7.8 | 7.6 | 8.4 | 7.7 | 7.6 | 8.0 | 8.3 | 8.0 | 7.1 | 7.7 | 7.8 | 7.8 | 8.1 | 7.7 |
| Pelvic fin: | | | | | | | | | | | | | | | | | |
| length of base | 4.6 | 4.2 | 4.5 | 4.2 | 4.2 | 4.0 | 4.7 | – | 4.6 | 5.1 | 4.7 | 4.5 | 4.3 | 4.2 | 4.8 | 4.3 | 4.3 |
| length of anterior margin | 4.9 | 4.7 | 4.8 | 4.3 | 4.5 | 4.4 | 4.8 | 4.7 | 4.6 | 4.3 | 4.9 | 4.2 | 4.0 | 4.5 | 4.2 | 4.5 | 4.4 |
| length of distal margin | 4.1 | 4.1 | 4.0 | 4.4 | 4.4 | 4.6 | 4.2 | 4.0 | 4.2 | 4.5 | 4.1 | 4.5 | 4.4 | 4.1 | 4.2 | 4.9 | 4.1 |
| length of claspers | 2.2 | – | 2.3 | 2.2 | 2.3 | – | 2.8 | – | 3.1 | 8.3 | 3.4 | 8.4 | – | – | 7.2 | – | – |
| Caudal fin: | | | | | | | | | | | | | | | | | |
| length of upper lobe | 26.1 | 26.4 | 27.5 | 27.6 | 26.3 | 25.8 | 25.8 | 26.0 | 27.0 | 26.6 | 26.3 | 25.0 | 23.6 | 24.1 | 24.4 | 25.3 | 24.9 |
| length of lower lobe | 10.3 | 10.1 | 11.5 | 10.7 | 9.4 | 10.5 | 9.5 | 10.8 | 10.4 | 10.1 | 10.0 | 9.3 | 9.4 | 9.4 | 9.6 | 10.5 | 9.2 |
| length from tip to notch | 6.0 | 5.8 | 5.7 | 5.7 | 6.3 | 6.2 | 6.2 | 6.0 | 6.6 | 6.2 | 5.8 | 5.9 | 5.9 | 5.2 | 5.8 | 5.9 | 5.7 |
| notch depth | 2.7 | 3.4 | 3.7 | 3.6 | 3.1 | 3.2 | 2.8 | 3.3 | 3.1 | 2.9 | 3.5 | 2.8 | 2.7 | 2.8 | 2.5 | 2.5 | 2.7 |

[1] Neotype of *Scoliodon sorrakowa*.
[2] Holotype of *Scoliodon longmani*.
[3] Holotype of *Scoliodon vagatus*.

The nominal subgenus *Rhizoprionodon* has a circumtropical distribution with the exception of Oceania. The subgenus *Protozygaena* is found in the western south Atlantic and the Indo-Pacific exclusive of Oceania and the coasts of Africa.

***Rhizoprionodon (Rhizoprionodon) acutus* (Rüppell)**

FIGURES 5, 6

"Sorra Kowah" Russell, 1803, Descriptions and figures of two hundred fishes . . . Coromandel, vol. 1,p. 9, fig. 15 (a common name).

*Carcharias acutus* Rüppell, 1835, Fische des rothen Meeres, p. 65, pl. 18, fig. 4 (market at Djetta; lectotype designation in Klausewitz, 1960, Senck. Biol., vol. 41, nos. 5, 6, p. 292).

*Carcharias sorrakowa* Bleeker, 1853, Verh. Bataviaasch Gen., vol. 25, p. 9 (Vizagapatam, based on "Sorra Kowah" Russell; see nomenclatural discussion under *Scoliodon laticaudus*).

*Carcharias (Scoliodon) walbeehmi* Bleeker, 1856, Nat. Tijdschr. Ned. Ind., vol. 10, p. 253 (Bintang).

*Carcharias (Scoliodon) crenidens* Klunzinger, 1879, Sitzb. Akad. Wiss. Wien, vol. 80, p. 426, pl. 8, fig. 3 (Queensland).

*Scoliodon longmani* Ogilby, 1912, Mem. Queensland Mus., vol. 1, p. 30 (Moreton Bay).

*Scoliodon vagatus* Garman, 1913, Mem. Mus. Comp. Zool., vol. 36 (text), p. 116 (Zanzibar).

*Carcharias eumeces* Pietschmann, 1913, Jahrb. Nassauischen Ver. Naturk., vol. 66, p. 172, p. 1 (Bibundi).

DIAGNOSIS.—Upper labial furrow well developed, 1.4 to 2.0 percent of t.l.; precaudal centra markedly elongate in posterior monospondylous region (as in plate 2A); precaudal vertebrae less in number than caudal vertebrae (equal in 1 out of 124 specimens); anterior margin of pectoral fin usually equal to, or shorter than, total length of first dorsal fin (79 out of 102 specimens); snout in front of nostrils 4.6–5.4 percent of t.l. in specimens less than 575 mm. t.l. (54 specimens; 4.0–4.5 percent in 8 specimens); 4.2–5.1 percent in specimens over 575 mm. t.l.; total teeth in outer row of upper jaw usually 25 (63 specimens out of 75); total teeth in outer row of lower jaw usually 24 (66 specimens out of 74); total enlarged hyomandibular pores usually more than 16 (110 out of 118 specimens); first dorsal origin usually slightly in advance of level of appressed pectoral inner corner (ranging to just behind inner corner); origin of second dorsal fin ranges from above posterior third of anal base to over anal axil; tip of appressed pectoral fin usually reaches to below, or beyond level of, the anterior third of the first dorsal base (infrequently only to the anterior fifth). Males maturing only at sizes over 600 mm.

DESCRIPTION (see also table 10).—Precaudal vertebrae 55–79 (table 9); caudal vertebrae 64–83; total vertebrae 121–162; upper teeth 11–1–11 to 13–1–13 (usually 12–1–12); lower teeth 11–11 to 13–13 (usually 12–12); cusps of some upper teeth in large specimens faintly

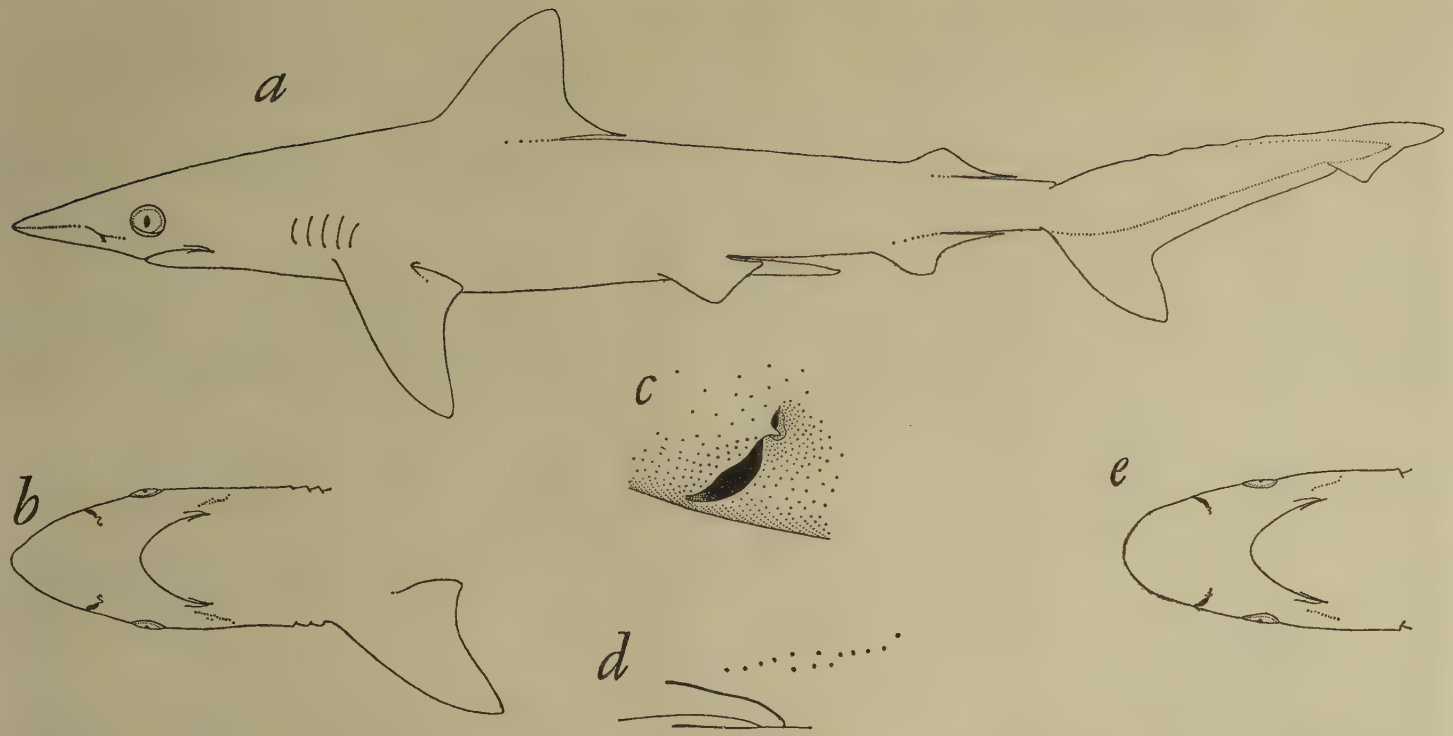


FIGURE 5.—*Rhizoprionodon acutus*, HUI E57/664, 624 mm. t.l., mature male from the Red Sea: *a*, left side; *b*, underside of head; *c*, enlarged right nostril; *d*, enlarged left labial furrows and adjacent enlarged hyomandibular pores; *e*, USNM 197343, 635 mm. t.l., female from the Red Sea, underside of head (*b* and *e* indicate the range of variation in snout shapes).

to moderately serrulate; cusps of lower teeth adumbrating this condition; dentition of mature males and females similar; sometimes cusps of teeth of mature males slightly more erect than those of females.

Denticles imbricate, 3-ridged and 3-toothed in young, 3- to 5-ridged and 3-toothed or with irregular posterior margin in adults.

Color of preserved specimens quite variable. Body gray, purplish gray, gray brown or buff brown above, pale below. Pectorals dark with a pale distal edge; pelvics and anal pale or dusky; upper caudal lobe usually with a dark edging in young; edging present or absent in adults; lower caudal lobe without a dark edging; other fins uniformly dark.

A low and poorly developed interdorsal ridge present or absent. Both precaudal pits present, the upper better developed.

Growth changes: There is a general tendency for distance from snout tip to outer nostrils, eye, mouth, and pectoral origin to decrease in percent of t.l. with increased t.l.; eye diameter, second dorsal base, and caudal notch depth decrease similarly. Distance from snout tip to second dorsal origin, anal origin, upper and lower caudal lobe origins tend to increase in percent of t.l. with increased t.l.

In large specimens there is a tendency for the axis of the upper caudal lobe to become raised in relation to the horizontal axis of the body.

The smallest mature male examined was 624 mm. t.l. from Eritrea. In general, males apparently mature at smaller sizes in the Red Sea than elsewhere, as seen in following tabulation:

| *Locality* | *T.L.* | *Clasper Length (%)* | *Locality* | *T.L.* | *Clasper Length (%)* |
|---|---|---|---|---|---|
| Philippines | 271 | 3.0 | Red Sea | 442 | 2.3 |
| Philippines | 280 | 2.9 | Red Sea | 445 | 2.2 |
| Philippines | 283 | 2.4 | India | 446 | 2.6 |
| Formosa (embryo) | 285 | 2.4 | Australia | 455 | 3.1 |
| Philippines | 288 | 2.7 | Senegal | 490 | 2.6 |
| Philippines | 296 | 2.8 | Australia | 500 | 2.8 |
| Philippines | 299 | 2.1 | Persian Gulf | 510 | 2.2 |
| Philippines | 304 | 2.3 | Madagascar | 510 | 2.3 |
| Nigeria | 352 | 2.2 | Philippines | 519 | 2.4 |
| Gulf of Aden | 331 | 2.9 | Australia | 520 | 2.2 |
| North Borneo | 335 | 2.3 | Red Sea | 560 | 2.2 |
| Philippines | 343 | 2.6 | Persian Gulf | 568 | 3.1 |
| Philippines | 350 | 3.1 | Japan | 576 | 2.5 |
| Nigeria | 353 | 2.2 | Ghana | 609 | 2.8 |
| India | 358 | 2.2 | Red Sea | 624 | 8.3 |
| Australia | 368 | 2.0 | Australia | 672 | 6.6 |
| India | 378 | 2.3 | Red Sea | 678 | 8.4 |
| Philippines | 391 | 1.9 | Liberia | 678 | 3.4 |
| Senegal (embryo) | 409 | 2.2 | South Africa | 692 | 3.4 |
| Australia | 440 | 2.1 | Senegal | 696 | 7.4 |

| Locality | T.L. | Clasper Length (%) | Locality | T.L. | Clasper Length (%) |
|---|---|---|---|---|---|
| Philippines | 709 | 7.6 | Senegal | 789 | 8.2 |
| Philippines | 722 | 8.0 | Macassar | 794 | 8.4 |
| Australia | 760 | 7.3 | Australia | 800 | 7.2 |
| French Equatorial Africa | 775 | 7.1 | Gulf of Thailand | 816 | 7.3 |
| | | | Australia | 874 | 6.9 |

The largest embryos seen were 409–411 mm. from Senegal; the smallest non-embryos from Senegal were 401–409 mm., and the smallest, from nearby Ghana and Nigeria, 308–320 mm. The smallest non-embryo examined was 242 mm. from the Philippines, where specimens under 300 mm. were not uncommon. The largest specimen examined from the Philippines was 722 mm. whereas the large embryos from Senegal were taken from a female 940 mm. (not seen by me). These figures may indicate that there are geographic populations varying in sizes attained, as well as indicating variation in size at birth in a given locality.

Geographic variation is indicated also in table 9, where groupings of precaudal vertebral numbers seem markedly different from one locality to another. The pattern of this variation is difficult to follow and will necessitate the examination of large numbers of specimens from many localities before it can be resolved.

Specimens from the Red Sea are noticeable for considerable variation in snout shape, ranging from rather acute to bluntly rounded. Also seen were some small west African specimens that had blunt snouts. Specimens with either acute or bluntly rounded snouts had the same relative snout lengths.

Some figures are available on the variation of precaudal vertebral counts in embryonic siblings and their mothers. A female from the Persian Gulf had 70 precaudal vertebrae; her two embryos had 68 and 72 precaudal vertebrae. A female from the Red Sea had 65 precaudal vertebrae and her three embryos had 68, 68, and 70 precaudal vertebrae. Three embryonic siblings from Senegal had 69, 69, and 70 precaudal vertebrae, and three from Durban, South Africa, had 71, 72, and 75 precaudal vertebrae.

Distribution.—This species is widely distributed from the Madeira Islands to Australia and Japan.

Relationships.—Within the subgenus *Rhizoprionodon*, *R. acutus* is most closely related to *R. porosus* and *R. terraenovae*, from which *R. acutus* differs in having a typically longer snout in front of the nostrils (fig. 1) and a higher dorsal-pectoral ratio (table 3).

Nomenclatural discussion.—The reasoning for placing *Scoliodon sorrakowa* Bleeker (1853) into the synonymy of *R. acutus* is given in the nomenclatural discussion of *Scoliodon laticaudus* (p. 580). Inas-

much as Bleeker's name is based on a Russell (1803) species for which no type material is available, I here designate SU 30502, a 368 mm. immature male, as neotype of *Scoliodon sorrakowa* (label data with the specimen is as follows: "*Scoliodon walbeehmi*, Madras Presidency, India. Coll. Madras Fisheries Dept., 1923, Herre 1934 Expeditions. Vizagapatam, Research. Madras, 1933"). The neotype is from the same general locality as the holotype and it conforms to Russell's figure and description except that it is approximately 9 mm. longer than the holotype.

I have examined all the type material of the nominal forms placed into the synonymy of *R. acutus* and find no reason for maintaining any as distinct from that species.

MATERIAL.—MADEIRA: ISZZ 7593 (1: 415 mm.). SENEGAL: MNHN A8005 (1: ca. 435); Goree, IFAN [no number] (2: 409–411, embryos), IFAN [no number] (1: 789), ZSZM 6288 (1: 401); St. Louis, NMV [no number] (1: 490); Dakar, IRSN 8.395 (1: 696); Joal, USNM 196156 (1: 354, embryo). FRENCH GUINEA: Sobane, USNM 196155 (1: 409); Konkoure, Mundung, ISH 296/59 (2: 426–435); Tamara Island, IRSN 6.907 (1: 516). LIBERIA: Kru Station, USNM 179719 (1: 387); Bushrod Island Beach, USNM 179718 (1: 678). GHANA: Elmina, Ashantee, USNM 42247 (1: ca. 310), USNM 42212 (1: ca. 320); Prampram, BMNH 1939.7.12.1 (1: ca. 770); Accra, BMNH 1930.3.24.1 (1: 609). NIGERIA: Lagos, BMNH 1937.4.19.1–2 (2: 308–352), BMNH 1936.8.20.1 (1: 477). CAMEROON: Bibundi, SMW 931 (1: ca. 495, holotype of *Carcharias eumeces*), NMV [no number] (1: ca. 488). FRENCH EQUATORIAL AFRICA: 29 miles south of Cape Lopez, MRAC 80253 (1: ca. 856), MRAC 80253 (1: 775); 11 miles south of Cape Lopez, IRSN 8.391 (1: 823). ANGOLA: 20 miles west northwest of Moanda, IRSN 8.393 (1: 445); 12 miles west of Moanda, MRAC 80252 (1: 466); south of Safaire, MRAC 80172 (1: 356); 8 miles west of Rio Cuanza, IRSN 8.390 (1: ca. 810). UNION OF SOUTH AFRICA: Durban, ANSP 73239 (1: 692), UND 82A–C (3 embryos). PORTUGUESE EAST AFRICA: Delagoa Bay, ANSP 55297 (1: 355). MOZAMBIQUE: Beira, DIRU 12 (1: 489). MADAGASCAR: east coast, ZSZM 7379 (1: ca. 378); Tamatave, NMV [no number] (1: 510). ZANZIBAR: MCZ 401 (1: 817, holotype of *Scoliodon vagatus*), MCZ 24 (1: ca. 610). GULF OF ADEN: Aden Harbor, RNH 12384 (2: 310–331). RED SEA: USNM 47603 (1: 553). ERITREA: HUI E57/660 (1: 730, and three embryos), HUI E57/658 (1: 649), HUI E57/662 (1: 646), HUI E57/661 (1: 669), HUI E57/659 (1: 721), HUI E57/663 (1: 678), HUI E57/666 (1: 445), HUI E57/664 (1: 624); near Massawa, USNM 197343 (1: 635); Hanfilah, Hasein Island [Dahlak Archipelago], NMV [no number] (1: 761). SAUDI ARABIA: Djetta [Jidda], NFIS 2783 (1: ca. 440, lectotype of *Carcharias acutus*, stuffed), NFIS 761 (2: 442–448).

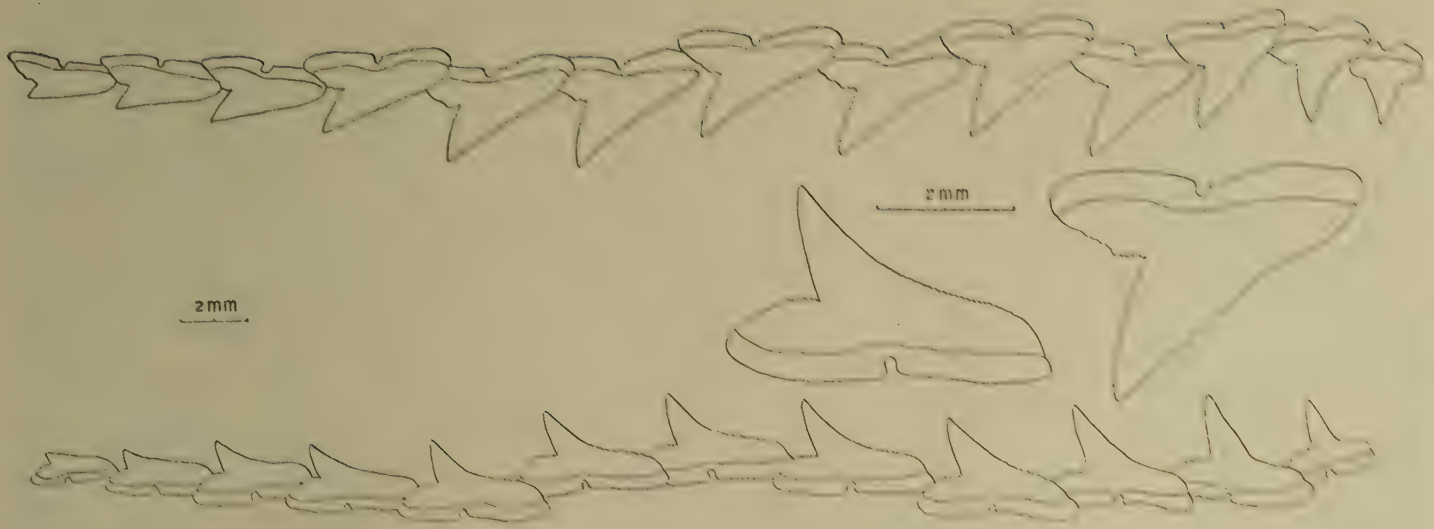


FIGURE 6.—*Rhizoprionodon acutus*, USNM 176744, 800 mm. t.l., mature male from Australia, right upper and lower teeth (symphysis to the right; inserted teeth are enlarged fifth upper and lower teeth from the right).

SUEZ: NMV [no number] (1: 560). GULF OF OMAN: Muscat, BMNH 1892.1.16.9–10 (1: 706). PERSIAN GULF: Ras el Mustaf, UZMK CN4 (1: 510); Jabrin, UZMK CN3 (1: 500); Tarut Bay, Zaal Island, USNM 148103 (1: 658), USNM 148104 (1: 690, and two embryos). INDIA: Malabar, BMNH 1889.2.1.4167–9 (1: 302); Calicut, SU 41986, in part (1: 371); Krusdai Island, Gulf of Manar, SU 41985 (1: 378); Madras, NFIS 4027 (1: 365), RNH 8575 (1: 341); Madras Presidency, SU 30502 (1: 368, neotype of *Scoliodon sorrakowa*): Pondicherry, MNHN 946, in part (1: 448); 50 miles from Ceylon, NMV [no number], in part (1: 338). ANDAMAN ISLANDS: BMNH 1870.6.14.21 (1: 360). THAILAND: NMV [no number] (2: 335–362); Bangkok, UZMK P0521 (1: 404): 13°09–13′ N. and 100°52–55′ E., 3–4 miles offshore, GVF 1557 (1: ca. 840); 12°30–40′ N. and 101°00–25′ E., GVF 1565 (2: 816–882). MALAYA: Singapore, NMV [no number] (1: 317), BMNH [no number] (1: 360). BINTANG ISLAND: BMNH 1867.11.28.191 (1: 440, female, holotype of *Carcharias* (*Scoliodon*) *walbeehmi*; no locality listed with specimen, but Bleeker described the species from a female, 453 mm., from Bintang); Rio, RNH 7368 (1: 421, female listed as holotype of *C.* (*S.*) *walbeehmi*, but I consider the difference in lengths too great to recognize this specimen as holotype). SUMATRA: Padang, NMV [no number] (1: ca. 790, and three embryos). MACASSAR: BMNH 1872.3.12.3 (1: 794). BATJAN [BACHAN] ISLAND: ISZZ 7674 (1: 321). ARU ISLANDS: near Meriri, NFIS 4026 (1: 450). AUSTRALIA: Northern Territory: Little Lagoon, northwest end of Groote Eylandt, Gulf of Carpentaria, USNM 174076 (1: 500); Bay of Yirrkalla, Northwest of Cape Arnhem, USNM 174077 (1: 785); Queensland: SMNS 2449 (1: ca. 575, holotype of *Carcharias crenidens*); Townsville, QMB I6190 (1: 672); Cape Cleveland, QMB I7034 (1: 874); Salamander Rocks, QMB I7136 (1: 440); Lindeman Island, AMS IA6159 (1: 760), AMS IA6681 (1: ca. 205, embryo); Brisbane, USNM 176744 (1: 800); Moreton Bay, QMB I12/292 (1: 455, holotype of *Scoliodon longmani*), AMS I12621 (1: 337); Moreton Island, DHMB 368 (1: 520); Deception Bay, QMB I8241 (1: 368), I8240 (1: 342). PHILIPPINES: MCZ 484 (1: 284): Sitankai, SU 13725 (1: 686); south Tumindao Lagoon, USNM 151235 (1: 716); Mindanao, SU 13152 (1: 722); Panay: Iloilo, SU 14454 (1: ca. 410); Capiz, SU 26862 (1: ca. 280); Unisan, Tayabas, SU 26820 (1: ca. 298); Luzon: Cavite, SU 9639 (2; 271–342); Orion, Bataan Province, ANSP 52798 (1: 481), ANSP 86371 (1: 242); Manila, UZMK 385 (1: 358), UZMK 386 (1: 277), SU 20592 (3: 283–296); Manila Bay: SU 26818 (3: 283–291), CNHM 46987 (1: 335), CNHM 46993 (1: 350), UWS 8568 (1: 299), SU 29621 (4: 258–304); La Monja Island, USNM 151234 (1: 709); Manila, fish market, USNM 151236 (2: 470–519), USNM 151238

(1: ca. 343), USNM 151239 (1: ca. 332). NORTH BORNEO: Sandakan, CNHM 23259 (1: 372), USNM 151237 (1: ca. 301), SU 27725 (2: 335–416), CNHM 21880 (1: ca. 420). SARAWAK: Santubong, BMNH 1894.1.19.88 (1: 420). FORMOSA: Tam Shui [Tanshui] ,Taipei Hsien, USNM 191192 (1: 820); Takao [Kashiung], CNHM 52099 (1: 285, embryo), CNHM 59261 (1: 909). JAPAN: BMNH 1862.11.1.80–132 (1: 576). HELGOLAND [undoubtedly an error]: SMNS 139 (1: 400).

### *Rhizoprionodon (Rhizoprionodon) terraenovae* Richardson

PLATE 2A

*Squalus (Carcharias) terraenovae* Richardson, 1836, Fauna Boreali Americana, vol. 3, p. 289 (off Newfoundland).

DIAGNOSIS.—Upper labial furrow well developed, 1.6–2.2 percent of t.l.; precaudal centra markedly elongate in posterior monospondylous region (plate 2A); precaudal vertebrae less in number than caudal vertebrae; anterior margin of pectoral fin usually longer than total length of first dorsal fin (32 out of 37 specimens); snout in front of nostrils 3.8–4.5 percent of t.l. in specimens less than 575 mm. t.l., 3.6–4.0 percent of t.l. in specimens over 575 mm. t.l.; total teeth in outer row of upper jaw usually 25 (18 out of 20 specimens); total teeth in outer row of lower jaw usually 24 (18 out of 20 specimens); total enlarged hyomandibular pores on both sides of head usually more than 16 (52 out of 53 specimens); first dorsal origin usually over, or in advance of, level of appressed pectoral inner corner (ranging to slightly behind inner corner); origin of second dorsal fin ranges from above midpoint of anal base to over posterior fifth of anal base; tip of appressed pectoral fin reaches beyond level of anterior third of first dorsal base. Males maturing at sizes over 640 mm.

DESCRIPTION (see also table 11).—Precaudal vertebrae 58–66 (66 in only 1 specimen out of 74; table 12); caudal vertebrae 67–81; total vertebrae 126–144; upper teeth 11–1–12 to 13–1–13 (usually 12–1–12); lower teeth 12–12 to 13–13 (usually 12–12); cusps of some upper teeth in large specimens faintly to moderately serrulate; cusps of lower teeth adumbrating this condition; dentition of mature males and females similar (at least to sizes of about 840 mm.); enlarged hyomandibular pores 8–18 on each side of head.

Denticles imbricate, 3-ridged and 3-toothed in young; 3- to 5-ridged and 3- to 5-toothed or irregularly margined in adults.

Color of preserved specimens variable: Body slate gray, buff or gray brown above, large specimens frequently with a few scattered round pale spots about one-third eye diameter; body pale below. Pectorals dark with pale distal edges; pelvics and anal pale or dusky; caudal dark with a black border, except for anterior and sometimes

TABLE 11.—*Proportional dimensions in percent of total length of* Rhizoprionodon terraenovae

| | ♂ 335 mm. Florida USNM 158479 | ♀ 341 mm. Texas USNM 116448 | ♀ 354 mm. Texas USNM 116448 | ♂ 362 mm. Texas USNM 116448 | ♂ 365 mm. Texas USNM 116448 | ♀ 390 mm. Texas USNM 116488 | ♀ 555 mm. Louisiana USNM 127128 | ♀ 557 mm. Louisiana USNM 127119 | ♂ 621 mm. Florida USNM 196168 | ♀ 827 mm. Texas USNM 127105 |
|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | |
| outer nostrils | 4.2 | 4.4 | 4.0 | 4.2 | 4.2 | 3.9 | 4.0 | 3.8 | 3.8 | 3.9 |
| eye | 7.7 | 7.9 | 7.8 | 7.7 | 7.6 | 7.0 | 7.3 | 7.4 | 6.8 | 7.0 |
| mouth | 8.6 | 8.8 | 8.8 | 8.7 | 8.4 | 8.2 | 7.9 | 7.8 | 7.3 | 7.4 |
| 1st gill-opening | 19.4 | 19.6 | 19.8 | 18.8 | 19.2 | 18.2 | 18.7 | 18.3 | 18.5 | 18.3 |
| pectoral origin | 22.4 | 22.9 | 21.8 | 21.8 | 22.5 | 21.3 | 22.2 | 21.8 | 21.1 | 21.2 |
| pelvic origin | 45.7 | 46.4 | 45.2 | 43.4 | 45.4 | 44.4 | 45.6 | 45.3 | 43.5 | 45.8 |
| 1st dorsal origin | 31.0 | 32.2 | 31.1 | 31.2 | 31.0 | 30.8 | 30.6 | 31.4 | 29.6 | 31.2 |
| 2nd dorsal origin | 61.5 | 63.3 | 62.4 | 61.6 | 63.0 | 62.8 | 63.2 | 63.8 | 63.0 | 63.7 |
| anal origin | 59.5 | 59.2 | 59.8 | 58.3 | 59.4 | 59.0 | 60.4 | 60.2 | 59.5 | 60.0 |
| upper caudal origin | 73.0 | 74.8 | 74.8 | 73.8 | 75.4 | 74.1 | 75.2 | 74.2 | 75.2 | 74.5 |
| lower caudal origin | 72.5 | 72.7 | 73.4 | 72.1 | 74.0 | 72.3 | 73.7 | 73.3 | 73.2 | 73.3 |
| Nostrils: | | | | | | | | | | |
| distance between inner corners | 5.4 | 5.7 | 5.5 | 5.5 | 5.5 | 5.3 | 5.2 | 5.0 | 4.4 | 4.7 |
| Mouth: | | | | | | | | | | |
| width | 7.8 | 7.4 | 6.9 | 6.9 | 7.1 | 7.4 | 7.1 | 7.0 | 6.9 | 6.9 |
| length | 4.5 | 5.0 | 4.7 | 4.7 | 4.9 | 4.5 | 5.2 | 4.9 | 4.3 | 4.5 |
| Labial furrow lengths: | | | | | | | | | | |
| upper | 1.7 | 2.2 | 2.0 | 2.1 | 1.9 | 1.8 | 2.0 | 1.9 | 2.1 | 1.7 |
| lower | 1.5 | 1.7 | 1.4 | 1.3 | 1.6 | 1.7 | 1.4 | 1.5 | 1.4 | 1.4 |
| Gill-opening lengths: | | | | | | | | | | |
| 1st | 2.1 | 1.8 | 1.9 | 1.9 | 1.9 | 1.7 | 1.8 | 1.8 | 1.9 | 1.8 |
| 2nd | 2.3 | 2.1 | 2.0 | 2.1 | 2.1 | 2.0 | 2.1 | 2.2 | 2.4 | 2.0 |
| 3rd | 2.4 | 2.2 | 2.3 | 2.2 | 2.2 | 2.2 | 2.2 | 2.3 | 2.5 | 2.2 |
| 4th | 2.1 | 2.0 | 2.2 | 1.8 | 2.1 | 2.0 | 2.1 | 2.3 | 2.3 | 2.1 |
| 5th | 1.5 | 1.7 | 1.7 | 1.3 | 1.7 | 1.6 | 1.6 | 1.8 | 1.8 | 1.7 |
| Eye: | | | | | | | | | | |
| horizontal diameter | 3.3 | 2.8 | 2.8 | 2.9 | 2.8 | 2.6 | 2.4 | 2.4 | 2.2 | 2.2 |
| 1st dorsal fin: | | | | | | | | | | |
| length of base | 9.0 | 9.3 | 9.2 | 9.1 | 9.0 | 9.0 | 8.6 | 9.0 | 8.9 | 9.6 |
| posterior margin | 3.9 | 3.8 | 4.0 | 3.9 | 3.6 | 3.8 | 3.7 | 4.2 | 3.6 | 3.9 |
| height | 7.4 | 8.1 | 7.4 | 8.0 | 7.7 | 8.4 | 8.1 | 8.1 | 8.0 | 9.2 |
| 2nd dorsal fin: | | | | | | | | | | |
| length of base | 3.0 | 2.9 | 3.2 | 3.2 | 3.2 | 3.0 | 2.8 | 2.7 | 2.9 | 3.0 |
| posterior margin | 4.5 | 4.7 | 4.2 | 4.7 | 4.2 | 4.5 | 4.5 | 4.8 | 4.5 | 5.0 |
| height | 2.0 | 2.2 | 2.0 | 2.2 | 1.9 | 2.1 | 2.2 | 2.3 | 1.9 | 2.5 |
| Anal fin: | | | | | | | | | | |
| length of base | 4.2 | 5.0 | 4.8 | 4.7 | 5.0 | 4.9 | 4.9 | 4.5 | 5.2 | 4.8 |
| posterior margin | 3.9 | 4.0 | 3.8 | 4.2 | 3.8 | 3.8 | 4.0 | 4.2 | 3.7 | 3.9 |
| height | 2.8 | 3.0 | 2.7 | 3.0 | 2.8 | 2.6 | 3.0 | 3.0 | 2.7 | 2.6 |
| Pectoral fin: | | | | | | | | | | |
| length of base | 5.1 | 5.0 | 5.1 | 5.3 | 5.4 | 4.8 | 4.9 | 5.3 | 5.4 | 5.1 |
| length of anterior margin | 12.8 | 12.8 | 12.4 | 12.8 | 13.3 | 13.2 | 13.6 | 14.4 | 13.9 | 13.7 |
| length of distal margin | 7.5 | 9.1 | 7.5 | 8.1 | 9.2 | 9.2 | 9.7 | 11.0 | 10.3 | 10.2 |
| width | 7.5 | 8.5 | 8.5 | 7.5 | 8.4 | 7.5 | 8.2 | 8.9 | 8.0 | 8.1 |
| Pelvic fin: | | | | | | | | | | |
| length of base | – | 4.2 | 4.5 | 4.3 | 4.1 | 3.9 | 4.6 | 4.5 | 4.2 | 4.4 |
| length of anterior margin | 4.8 | 5.2 | 5.4 | 5.4 | 4.5 | 5.0 | 4.4 | 5.4 | 4.7 | 5.0 |
| length of distal margin | 3.6 | 4.3 | 3.8 | 4.2 | 3.8 | 4.1 | 4.4 | 4.5 | 4.2 | 4.1 |
| length of claspers | 2.4 | – | – | 2.5 | 2.2 | – | – | – | 2.4 | – |
| Caudal fin: | | | | | | | | | | |
| length of upper lobe | 27.2 | 26.4 | 26.2 | 26.5 | 25.4 | 26.4 | 25.2 | 25.9 | 25.8 | 25.0 |
| length of lower lobe | 9.6 | 10.2 | 11.1 | 10.4 | 9.3 | 10.5 | 10.5 | 10.8 | 9.8 | 10.8 |
| length from tip to notch | 5.7 | 5.7 | 5.5 | 5.4 | 5.3 | 6.6 | 5.9 | 6.8 | 6.5 | 5.9 |
| notch depth | 3.6 | 3.6 | 3.6 | 3.6 | 3.3 | 3.6 | 3.3 | 3.2 | 3.0 | 2.7 |

posterior edge of lower lobe; first dorsal dark, sometimes with a darker posterior edging; second dorsal uniformly dark or black in adults, usually with an irregular blackening of the apex in young.

A low interdorsal ridge present in all well-preserved specimens examined. Both precaudal pits present, the upper better developed.

Growth changes: There is a general tendency for distance from snout tip to outer nostrils, eye, mouth, and first gill-opening to decrease in percent of t.l. with increased t.l. Distance between inner corners of nostrils, eye diameter, length of upper caudal lobe, and notch depth also decrease in similar manner. Distance from snout tip to second dorsal origin and length of anterior and distal margins of pectoral fin tend to increase in percent of t.l. with increased t.l.

In large specimens there is a tendency for the axis of the upper caudal lobe to become raised in relation to the horizontal axis of the body.

Insufficient information is available to establish the size at which males first mature, but based on the following tabulation, it appears that this size is greater than 640 mm. t.l.:

| *Locality* | *T.L.* | *Clasper Length (%)* | *Locality* | *T.L.* | *Clasper Length (%)* |
|---|---|---|---|---|---|
| Texas | 227 | 2.2 | Mississippi | 492 | 2.5 |
| Texas | 319 | 2.4 | South Carolina | 498 | 2.6 |
| North Carolina | 324 | 2.5 | South Carolina | 545 | 2.6 |
| Alabama | 329 | 2.4 | Florida | 545 | 2.5 |
| Florida | 335 | 2.4 | Florida | 621 | 2.4 |
| Texas | 341 | 2.0 | Georgia | 631 | 2.5 |
| Florida | 345 | 2.2 | New Jersey | 642 | 2.9 |
| Florida | 348 | 2.5 | Louisiana | 647 | 2.9 |
| Texas | 362 | 2.5 | Yucatan | 810 | 8.3 |
| Texas | 365 | 2.2 | Florida | 843 | 7.1 |
| North Carolina | 378 | 2.0 | Florida | ca. 915 | ca. 8.0 |

The smallest non-embryo examined was 227 mm. and the largest embryo was 292 mm. The largest specimen seen was about 915 mm., but it seems probable that specimens reach approximately 1000 mm. Bigelow and Schroeder (1948) reported specimens of 930 mm., but whether these were *R. terraenovae* or *R. porosus* is not clear.

Only one female with embryos was examined for precaudal vertebrae counts. The female had 59 and the embryos 59 and 60. Three other sibling embryos each had 60 precaudal vertebrae.

Distribution and nomenclatural discussion.—Northeastern coasts of North America from the Bay of Fundy south to Yucatan, Mexico. The species was described from a specimen from Newfoundland, but Jordan and Evermann (1896) and Bigelow and Schroeder (1948) believe that this is in error and that the specimen is from the southern United States (reasons not stated). No other specimens

are recorded from Newfoundland and this assumption may be correct; however, the type specimen is not known to exist and it is not possible to discern from the description just what species of *Rhizoprionodon* Richardson might have had. Since the name has been used widely for the North American species, it seems best to retain it here.

The species occurs in marine and brackish waters at depths (over depths?) as great as 153 fathoms.

RELATIONSHIPS.—*Rhizoprionodon terraenovae* and *R. porosus* are cognate species. The separation of these two species is based on precaudal vertebral numbers (table 12) that are correlated with geographically non-overlapping distributions of the species. Some minor proportional differences are indicated in tables 11 and 13, but since these are small, they seem scarcely of value in recognizing the species.

The explanation for the existence and distribution of two cognate species such as *R. terraenovae* and *R. porosus* is not clear. The Pleistocene glacial relict theory of Walters and Robins (1961) does not seem to apply here as the two species apparently are common in both the tropical and temperate portions of their distributions. Continued separation is also a problem. The species are essentially shallow-water forms, but some specimens of each species have been taken well out to sea and in waters of great depth (see *R. porosus*). Even if depth and expanses of water hindered mixing of the two species, it would still be necessary to explain why they have not invaded each other's territory from the Central American coast, where *R. terraenovae* is reported from Yucatan and *R. porosus* from Honduras.

*Rhizoprionodon terraenovae* and *R. porosus* are related closely to *R. acutus*, from which they differ primarily in having a shorter snout length (fig. 1) and a lower dorsal-pectoral ratio (table 3).

MATERIAL.—NEW BRUNSWICK: Bay of Fundy, Grand Manan Island, MCZ 178 (1: 400 mm.). NEW JERSEY: Holly Beach, ANSP 22058 (1: 642). MARYLAND: Baltimore, UZMK 358 (1: ca. 488). VIRGINIA: Chesapeake Bay, Cape Charles, USNM 42491 (1: 530). NORTH CAROLINA: MCZ 1320 (3: 296–362), NMV [no number] (6: 355–370); Fort Macon, ANSP 561 (1: ca. 285), MCZ 35209 (2: 313–341); Beaufort, USNM 51892 (1: 378), USNM 51879 (1: 324), CAS 19777 (1: 344). SOUTH CAROLINA: Charleston, USNM 25181 (4: 437–545), MCZ 712 (1: 312); 33°38′ N. and 77°36′ W., USNM 38511 (1: ca. 785). GEORGIA: 33°52′ N. and 78°13′ W., 5 fathoms, USNM 196179 (1: 631). FLORIDA: USNM 39350 (1: ca. 915, skin); 29°47′ N. and 80°12′ W., 145–153 fathoms, USNM 158479 (1: 335); Indian River, USNM 7306 (4: ca. 333-ca. 375); 24°44′ N. and 80°43′ W., 30 fathoms, USNM 196801 (1: 758); Key West, USNM 125883 (1: 550); Tortugas, USNM 61126 (1: 228, embryo); west coast at 26°10′ N., 26 fathoms, USNM 196168 (1: 621); west coast at 26°44′ N., 29.5

TABLE 12.—*Frequency distribution of precaudal vertebrae number in* Rhizoprionodon terraenovae *and* R. porosus

| | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *R. terraenovae* | | | | | | | | | | | | | | | | | | |
| Bay of Fundy | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| New Jersey | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Maryland | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Virginia | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – |
| North Carolina | – | – | 1 | – | 5 | 2 | 2 | 3 | 1 | – | – | – | – | – | – | – | – | – |
| South Carolina | – | – | 1 | 1 | 1 | 2 | – | 1 | – | – | – | – | – | – | – | – | – | – |
| Georgia | – | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – |
| Florida | | | | | | | | | | | | | | | | | | |
| East Coast | – | – | – | 2 | – | 1 | 1 | 1 | – | – | – | – | – | – | – | – | – | – |
| Keys | – | – | – | 2 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| West Coast | 1 | 3 | 1 | 1 | 1 | 1 | 1 | – | – | – | – | – | – | – | – | – | – | – |
| Alabama | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Mississippi | – | – | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Louisiana | 1 | – | 1 | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Texas | 2 | – | 5 | 9 | 5 | 3 | 1 | 1 | – | – | – | – | – | – | – | – | – | – |
| Yucatan | – | – | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Total | 4 | 5 | 10 | 16 | 16 | 11 | 5 | 6 | 1 | | | | | | | | | |
| *R. porosus* | | | | | | | | | | | | | | | | | | |
| Bahamas | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 2 | 1 | – |
| Cuba | – | – | – | – | – | – | – | – | – | – | – | 2 | 1 | – | – | – | 2 | – |
| Jamaica | – | – | – | – | – | – | – | – | – | 1 | – | – | 1 | 2 | 3 | – | 4 | – |
| Hispaniola | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | 2 | 2 | 2 |
| Puerto Rico | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – |
| Virgin Islands | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – |
| Martinique | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – |
| Grenada | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – |
| Honduras | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – |
| Panama | – | – | – | – | – | – | – | – | – | – | – | 1 | 1 | – | – | – | – | – |
| Venezuela | – | – | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – |
| Brazil | – | – | – | – | – | – | – | – | 2 | 2 | 4 | 4 | 3 | 5 | 1 | 1 | – | – |
| Uruguay | – | – | – | – | – | – | – | – | – | – | 1 | – | – | – | – | – | 1 | – |
| Total | | | | | | | | | 2 | 3 | 5 | 7 | 8 | 8 | 7 | 5 | 11 | 2 |

fathoms, USNM 196267 (1: 843); Sanibel Island, San Carlos Bay, SU 36077 (1: 344); Clearwater, ANSP 40041 (1: 381); St. Marks, USNM 92231 (1: 345); Apalachicola Bay, near West Pass, USNM 125767 (1: 348), USNM 125764 (1: 337); Pensacola, USNM 30814 (1: 284, embryo), USNM 30706 (1: 545; 2 embryos: 280 and 292). ALABAMA: Mobile Bay, USNM 125873 (1: 329). MISSISSIPPI: Gulf coast, USNM 147773 (1: 492). LOUISIANA: half mile off Grand Isle, USNM 127127 (1: 647), USNM 127128 (1: 555), USNM 127129 (1: 549); two miles southeast of Grand Isle, USNM 127119 (1: 557). TEXAS: Harbor Island, USNM 127105 (1: 827); Galveston, USNM 116451 (13: ca. 299–ca. 374), USNM 116448 (5: 341–390), USNM 121618 (4: 227–341); Brownsville, USNM 171765 (3: ca. 275–ca. 285, embryos). MEXICO: south of Alacran Reef, one and a half miles off Yucatan, USNM 160830 (1: 810).

### *Rhizoprionodon (Rhizoprionodon) porosus* Poey

FIGURES 7, 8

*Squalus porosus* Poey, 1861, Memorias sobre la historia natural de Cuba, vol. 2, p. 339, pl. 19, figs. 11, 12 (Cuba).

DIAGNOSIS.—Upper labial furrow well developed, 1.8–2.3 percent of t.l. (1.3 and 1.5 in 2 out of 19 specimens); precaudal centra markedly elongate in posterior monospondylous region (as in Plate 2A); precaudal vertebrae less in number than caudal vertebrae; anterior margin of pectoral fin usually longer than total length of first dorsal fin (32 out of 35 specimens); snout in front of nostrils 3.7–4.5 percent of t.l. in specimens less than 575 mm. t.l.; 3.3–4.3 percent of t.l. in specimens over 575 mm. t.l.; total teeth in outer row of upper jaw usually 25 (19 out of 22 specimens); total teeth in outer row of lower jaw 24; total enlarged hyomandibular pores on both sides of head more than 17; first dorsal origin usually slightly behind, or over, level of appressed pectoral inner corner (ranging to slightly in advance of inner corner); origin of second dorsal fin ranges from above midpoint of anal base to over posterior fourth of anal base; tip of appressed pectoral fin reaches beyond level of anterior third of first dorsal base. Males maturing at a size between 575 and 644 mm.

DESCRIPTION (see also table 13).—Precaudal vertebrae 66–75 (66 in only 2 out of 58 specimens; table 12); caudal vertebrae 69–85; total vertebrae 136–159 (only 1 with less than 140); upper teeth 11–1–12 to 13–1–13 (usually 12–1–12); lower teeth 12–12; cusps of some upper teeth in large specimens faintly to moderately serrulate; cusps of lower teeth adumbrating this condition; dentition of mature males (one seen) and females similar; enlarged hyomandibular pores 9–19 on each side of head.

Denticles imbricate, 3-ridged and 3-toothed in young; 3- to 5-ridged and 3-toothed or irregularly margined in adults.

Color of preserved specimens similar to that in *R. terraenovae* (p. 601). Springer (1950) described the color of a fresh specimen (as *Scoliodon terraenovae*) from deep water off the Bahamas. It was characterized as having "unusually vivid markings of white spots and white edges on the fins."

A low interdorsal ridge present or absent. Both precaudal pits present, the upper best developed.

Growth changes: From the data at hand (table 13) growth changes do not appear to be as marked as in the cognate *R. terraenovae*. Such changes possibly are obscured because of the variability to be expected among insular populations and the great geographical range represented. In contrast, the *R. terraenovae* figures were obtained, with one exception, from Gulf of Mexico specimens. Such dimen-

TABLE 13.—*Proportional dimensions in percent of total length of* Rhizoprionodon porosus

| | ♂ 323 mm. Jamaica USNM 9342 | ♂ 400 mm. Haiti ANSP 91757 | ♀ 413 mm. Brazil MCZ 432 | ♀ 460 mm. Uruguay MCZ 525 | ♂ 490 mm. Cuba CAS IU139 | ♂ 501 mm. Jamaica USNM 30014 | ♂ 510 mm. Brazil USNM 43357 | ♀ 710 mm. Cuba USNM 19795 | ♀ 775 mm. Cuba USNM 33079 | ♀ 810 mm. Virgin Islands USNM 179846 |
|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | |
| outer nostrils | 4.2 | 4.0 | 4.2 | 4.1 | 3.7 | 3.8 | 4.1 | 3.9 | 3.9 | 3.8 |
| eye | 8.0 | 7.4 | 7.6 | 7.0 | 7.1 | 7.2 | 7.5 | 6.8 | 7.3 | 7.0 |
| mouth | 8.9 | 8.0 | 8.3 | 7.6 | 7.6 | 7.8 | 8.4 | 7.2 | 7.4 | 7.4 |
| 1st gill-opening | 20.8 | 17.7 | 17.7 | 17.4 | 18.4 | 17.6 | 18.6 | 17.3 | 17.4 | 17.7 |
| pectoral origin | 24.2 | 21.5 | 20.6 | 20.2 | 21.2 | 21.0 | 21.6 | 20.2 | 21.3 | 20.6 |
| pelvic origin | 47.6 | 44.5 | 46.0 | 45.6 | 44.9 | 45.7 | 45.7 | 45.8 | 48.0 | 45.2 |
| 1st dorsal origin | 32.5 | 27.0 | 29.6 | 29.8 | 29.2 | 29.8 | 31.4 | 29.4 | 31.8 | 30.0 |
| 2nd dorsal origin | 63.7 | 60.5 | 61.8 | 62.0 | 61.6 | 62.1 | 63.2 | 63.2 | – | 63.1 |
| anal origin | 61.2 | 57.6 | 59.4 | 59.1 | 59.2 | 60.1 | 60.2 | 60.5 | 62.5 | 60.0 |
| upper caudal origin | 75.2 | 72.7 | 73.9 | 73.9 | 73.5 | 73.4 | 74.9 | 75.2 | 76.4 | 74.4 |
| lower caudal origin | 73.9 | 71.5 | 72.6 | 72.1 | 72.2 | 71.6 | 73.7 | 74.0 | 75.0 | 73.5 |
| Nostrils: | | | | | | | | | | |
| distance between inner corners | 5.6 | 5.2 | 5.1 | 5.0 | 5.2 | 5.4 | 5.5 | 4.8 | 5.2 | 5.1 |
| Mouth: | | | | | | | | | | |
| width | 7.6 | 7.0 | 7.3 | 6.7 | 7.2 | 6.6 | 7.3 | 7.0 | 7.2 | 7.2 |
| length | 5.0 | 4.3 | 4.1 | 4.1 | 4.5 | 4.6 | 4.4 | 4.2 | 4.8 | 4.4 |
| Labial furrow lengths: | | | | | | | | | | |
| upper | 2.0 | 2.0 | 2.2 | 1.8 | 2.0 | 2.0 | 2.0 | 1.3 | 2.3 | 1.9 |
| lower | 1.8 | 1.6 | 1.4 | 1.3 | 1.5 | 1.3 | 1.5 | 1.4 | 1.6 | 1.6 |
| Gill-opening lengths: | | | | | | | | | | |
| 1st | 2.1 | 1.7 | 2.0 | 1.7 | 1.6 | 1.7 | 1.6 | 1.6 | 1.7 | 2.0 |
| 2nd | 2.4 | 1.9 | 2.1 | 1.9 | 1.9 | 2.0 | 2.1 | 1.9 | 2.0 | 2.1 |
| 3rd | 2.5 | 2.1 | 2.3 | 2.1 | 2.0 | 2.5 | 2.2 | 2.1 | 2.5 | 2.2 |
| 4th | 2.5 | 2.3 | 2.2 | 2.0 | 2.3 | 2.3 | 2.2 | 2.1 | 2.7 | 2.1 |
| 5th | 2.1 | 2.0 | 1.7 | 1.5 | 1.8 | 1.8 | 1.7 | 1.8 | 2.1 | 1.6 |
| Eye: | | | | | | | | | | |
| horizontal diameter | 3.4 | 2.7 | 2.8 | 2.4 | 2.8 | 2.6 | 2.6 | 2.2 | 2.1 | 2.0 |
| 1st dorsal fin: | | | | | | | | | | |
| length of base | 9.3 | 8.5 | 8.7 | 7.8 | 9.2 | 8.5 | 9.0 | 8.9 | 8.4 | 9.2 |
| posterior margin | 4.0 | 3.9 | 3.9 | 4.0 | 3.5 | 4.3 | 3.5 | 3.7 | 4.1 | 3.8 |
| height | 9.0 | 8.6 | 7.8 | 7.3 | 8.3 | 10.1 | 8.0 | 9.6 | 9.6 | 8.6 |
| 2nd dorsal fin: | | | | | | | | | | |
| length of base | 3.0 | 3.0 | 3.3 | 2.6 | 3.3 | 2.9 | 2.8 | 2.8 | – | 2.8 |
| posterior margin | 4.0 | 4.5 | 4.5 | 4.6 | 4.5 | 5.0 | 5.2 | 4.4 | 4.7 | 5.2 |
| height | 1.9 | 2.2 | 2.1 | 2.3 | 2.3 | 2.6 | 2.1 | 2.4 | 2.2 | 2.5 |
| Anal fin: | | | | | | | | | | |
| length of base | 4.5 | 4.4 | 4.9 | 4.1 | 4.1 | 4.4 | 4.5 | 4.2 | 4.0 | 4.7 |
| posterior margin | 3.4 | 4.1 | 3.9 | 4.3 | 3.6 | 4.2 | 4.3 | 3.9 | – | 4.3 |
| height | 2.8 | 3.2 | 3.1 | 3.2 | 2.9 | 3.2 | 2.7 | 3.0 | 3.0 | 2.8 |
| Pectoral fin | | | | | | | | | | |
| length of base | 5.1 | 4.2 | 4.9 | 4.8 | 4.6 | 4.5 | 4.8 | 4.5 | 5.0 | 5.0 |
| length of anterior margin | 13.4 | 13.2 | 13.3 | 11.2 | 13.9 | 14.1 | 13.1 | 13.9 | 14.7 | 14.4 |
| length of distal margin | 9.8 | 9.2 | 8.8 | 8.7 | 9.7 | 11.0 | 9.2 | 11.6 | 11.5 | 10.6 |
| width | 8.3 | 7.9 | 8.0 | 7.9 | 7.8 | 8.1 | 7.8 | 8.1 | 8.0 | 8.1 |
| Pelvic fin: | | | | | | | | | | |
| length of base | 4.0 | 4.0 | 4.0 | 3.5 | 3.2 | 4.2 | 3.6 | 4.2 | 4.7 | 4.1 |
| length of anterior margin | 4.2 | 4.9 | 4.5 | 3.9 | 4.3 | 5.0 | 4.4 | 4.5 | 4.5 | 4.6 |
| length of distal margin | 4.4 | 4.0 | 4.3 | 3.9 | 4.0 | 4.4 | 4.0 | 4.0 | 4.7 | 4.4 |
| length of claspers | 2.6 | 2.0 | – | 2.7 | 2.6 | 2.6 | 3.9 | – | – | – |
| Caudal fin: | | | | | | | | | | |
| length of upper lobe | 25.8 | 28.0 | 26.8 | 26.6 | 26.4 | 26.8 | 26.9 | 25.2 | 24.2 | 26.0 |
| length of lower lobe | 10.4 | 11.3 | 10.1 | 9.3 | 11.5 | 11.6 | 10.9 | 11.6 | 11.0 | 10.9 |
| length from tip to notch | 6.1 | 6.9 | 6.5 | 6.5 | 5.7 | 5.7 | 5.5 | 5.7 | 6.0 | 5.6 |
| notch depth | 3.4 | 3.3 | 3.4 | 3.1 | 2.8 | 3.1 | 3.1 | 2.6 | 2.7 | 3.1 |

sions as do show growth changes in *R. porosus* indicate a course of development similar to that found in *R. terraenovae*.

Only one mature male, 644 mm., was seen; the largest immature male was 575 mm. The following tabulation presents the available data on proportionate clasper lengths:

| Locality | T.L. | Clasper Length (%) | Locality | T.L. | Clasper Length (%) |
|---|---|---|---|---|---|
| Jamaica | 323 | 2.6 | Uruguay | 460 | 2.7 |
| Brazil | 340 | 2.4 | Uruguay | 472 | 2.2 |
| Brazil | 357 | 2.7 | Cuba | 490 | 2.6 |
| Panama | 376 | 2.1 | Jamaica | 501 | 2.6 |
| Brazil | 397 | 1.8 | Grenada | 501 | 1.9 |
| Brazil | 399 | 1.8 | Brazil | 510 | 3.9 |
| Haiti | 400 | 2.0 | Brazil | 514 | 2.4 |
| Brazil | 433 | 2.1 | Venezuela | 575 | 3.0 |
| Brazil | 434 | 2.0 | Brazil | 644 | 8.0 |

The smallest non-embryo seen was 310 mm. The largest embryo was 390 mm. The largest specimen examined was a stuffed female from Brazil, approximately 1050 mm.

Little data on sibling variation is available. Three embryos, presumably siblings, from Saba Bank had 72, 73, and 74 precaudal vertebrae. Two others from Cuba had 75 and 76 precaudal vertebrae.

DISTRIBUTION.—Essentially from the continental and insular shorelines of the western Atlantic between 24° N. and 35° S. latitudes. Backus (1957) reported taking a specimen (as *Scoliodon terraenovae*) from the surface about 65 miles north of Barbuda, where the depth was about 3300 fathoms.

RELATIONSHIPS.—See under *Rhizoprionodon terraenovae* (p. 604).

NOMENCLATURAL DISCUSSION.—It is not known whether a type exists for *S. porosus*. The illustrations of the teeth and the description are sufficient to establish that Poey had a species of *Rhizoprionodon*. Since only one species of *Rhizoprionodon* occurs in Cuba, I have elected to use Poey's name for it.

MATERIAL.—BAHAMAS: Bimini, USNM 196526 (1: 775 mm.); about three-fourths of a mile west of Riding Rock Light in 60 feet of water, UMML 10410 (2: 797–844). CUBA: USNM 9832 (2: ca. 248–ca. 251, embryos), USNM 19795 (1: 710), USNM 33079 (1: 775); Havana, CAS IU139 (1: 490), SU 10845 (1: 462), USNM 24793 (1: 758). JAMAICA: USNM 9342 (2: 323–388), USNM 30014 (1: 501), USNM 30059 (1: 380), SU 11825 (1: 461), SU 11826 (1: 518), SU 11827 (1: ca. 500), MNHN 1070 (1: ca. 430), NMV [no number] (1: ca. 385), CNHM 2797 (1: ca. 409), CNHM 2799 (1: ca. 503). HAITI: Port-au-Prince Bay, ANSP 91757 (3: ca. 310–400), USNM 133660 (2: 525–ca. 535). SANTO DOMINGO [DOMINICAN REPUBLIC]: ANSP 77115 (1: 584),

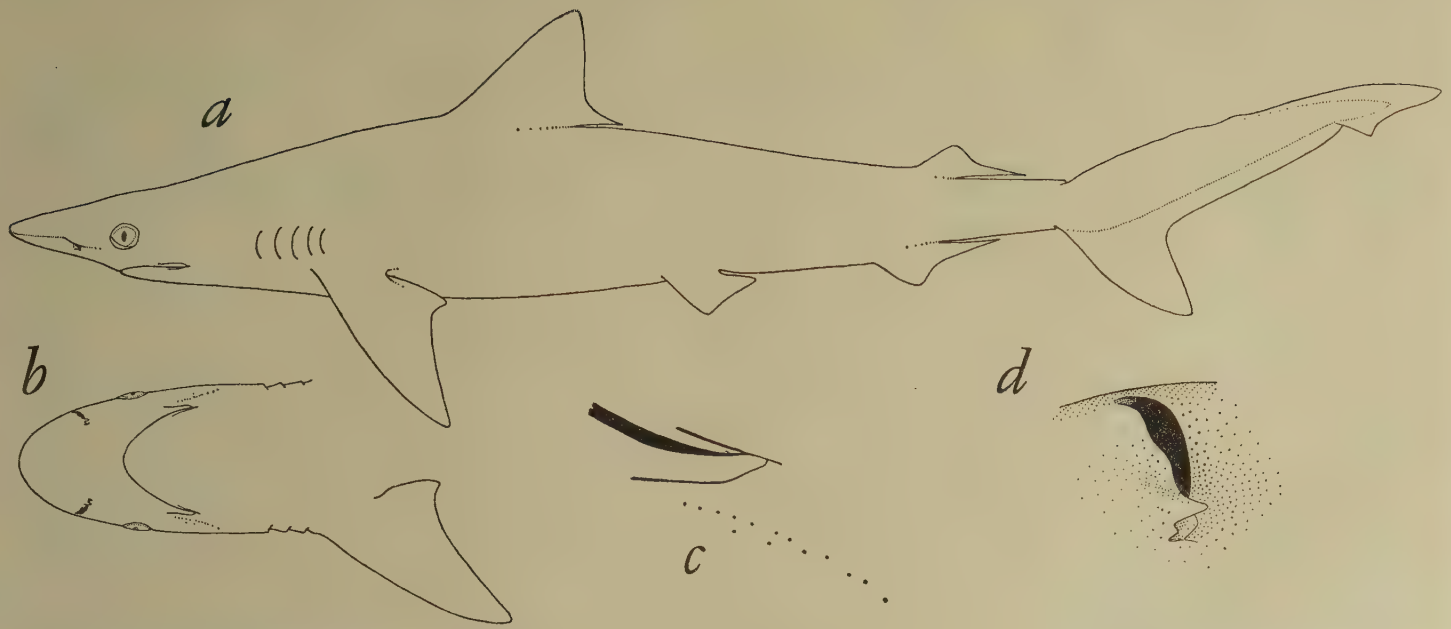


FIGURE 7.—*Rhizoprionodon porosus*, USNM 179846, 851 mm. t.l., female from the Virgin Islands: *a*, left side; *b*, underside of head; *c*, enlarged right labial furrows and adjacent enlarged hyomandibular pores; *d*, enlarged left nostril.

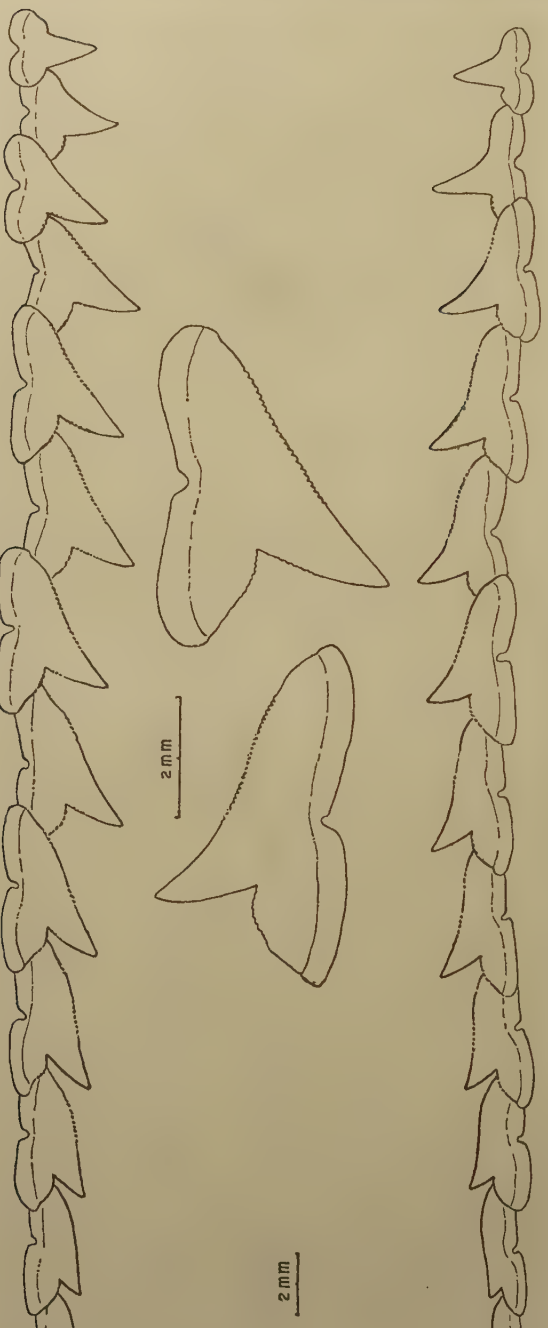


FIGURE 8.—*Rhizoprionodon porosus*, USNM 33079, 775 mm. t.l., female from Cuba, right upper and lower teeth (symphysis to the right; inserted teeth are enlarged fifth upper and lower teeth from the right).

NMV [no number] (1: 410). PUERTO RICO: west of El Mario, USNM 196613 (1: 472). VIRGIN ISLANDS: Booby Rock, St. John, USNM 179846 (1: 851). SABA BANK [ISLAND]: RNH 9270 (3: 380–390, embryos). GRENADA ISLAND: BMNH 1904.6.24.1 (1: 501). MARTINIQUE ISLAND: MNHN 1143 (1: 444). HONDURAS: USNM 44470 (1: 303). PANAMA: off reef at Ft. Sherman, AMNH 11413B (1: 333); Colón, market, USNM 79324 (1: 376). VENEZUELA: Caracas Bay, RNH 23321 (1: 575). BRAZIL: MNHN 3467 (1: ca. 1050, stuffed); Pernambuco, MCZ 714 (2: 340–376); Recife, high sea, SU 52747 (1: 343), SU 52857 (2: 390–434), SU 52858 (1: 397), SU 52859 (1: 366), SU 52860 (1: ca. 482); Bahía, USNM 43357 (1: 510), MNHN 1144 (1: 644), BMNH [no number] (1: 432); Rio de Janeiro, BMNH 1923.7.30.1 (1: 415), BMNH 1903.6.9.130–132 (2: 488–540), MCZ 720 (1: 357), MCZ 432 (2: 413–476), MCZ 160 (1: 514); Marica, SU 52748 (1: ca. 388); Santos, littoral of São Paulo, SU 52861 (1: 433); Maceio, SU 8446 (2: 370–399). URUGUAY: Maldonado, MCZ 525 (1: 460), NMV [no number] (1: 472).

### *Rhizoprionodon (Rhizoprionodon) longurio* (Jordan and Gilbert)

FIGURE 9

*Carcharias longurio* Jordan and Gilbert, 1882, Proc. U.S. Nat. Mus., vol. 5, p. 106 (Mazatlán).

DIAGNOSIS.—Upper labial furrow well developed, 2.1–2.6 percent of t.l.; precaudal centra markedly elongate in posterior monospondylous region (as in plate 2A); precaudal vertebrae ranging from 12 less to 8 more than caudal vertebrae; anterior margin of pectoral fin usually equal to, or shorter than, total length of first dorsal fin (27 out of 32 specimens); snout in front of nostrils 5.1–6.0 percent of t.l. in specimens less than 575 mm. t.l., 4.5–5.0 percent of t.l. in specimens over 575 mm. t.l.; total teeth in outer row of upper jaw usually 27 or 29 (29 specimens; 28 or 30 in 3 specimens); total teeth in outer row of lower jaw 26 (21 specimens; 27 or 28 in 11 specimens); total enlarged hyomandibular pores on both sides of head usually more than 16 (32 out of 33 specimens); first dorsal origin usually over, or slightly in advance of, level of appressed pectoral inner corner, infrequently slightly behind level of inner corner; origin of second dorsal fin occurs above posterior third of anal base and always in advance of anal axil; tip of appressed pectoral fin reaches to below level of anterior one- to two-thirds of first dorsal base. Males maturing at sizes over 600 mm.

DESCRIPTION (see also table 14).—Precaudal vertebrae 68–86; caudal vertebrae 73–85; total vertebrae 146–167; upper teeth 13–1–13 to 15–1–14; lower teeth 13–13 to 14–14 (higher and lower counts usually correlated); cusps of some upper teeth in large specimens slightly serrulate; cusps of lower teeth adumbrating this condition;

TABLE 14.—*Proportional dimensions in percent of total length of* Rhizoprionodon longurio

| | ♂351 mm. Mexico SIO H51-306 | ♀358 mm. Mexico SIO H51-306 | ♂402 mm. Mexico UCLA W52-246 | ♂418 mm. Mexico UCLA W52-246 | ♀517 mm. Mexico USNM 28306 [1] | ♀518 mm. Mexico USNM 29551 [1] | ♂583 mm. Panama USNM 78101 | ♂657 mm. Peru USNM 127756 | ♂688 mm. Peru USNM 127756 | ♂792 mm. Mexico USNM 28330 [1] |
|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | |
| outer nostrils | 5.3 | 5.1 | 5.8 | 5.8 | 5.5 | 5.2 | 4.9 | 4.6 | 4.9 | 4.5 |
| eye | 8.8 | 8.7 | 9.1 | 9.4 | 8.8 | 8.4 | 8.4 | 7.8 | 8.1 | 7.9 |
| mouth | 9.7 | 9.5 | 9.8 | 10.0 | 9.0 | 9.0 | 8.9 | 8.2 | 8.1 | 7.9 |
| 1st gill-opening | 20.5 | 19.8 | 21.4 | 21.3 | 20.3 | 20.2 | 21.3 | 20.8 | 20.4 | 19.6 |
| pectoral origin | 24.5 | 22.8 | 24.9 | 24.4 | 23.4 | 23.2 | 23.4 | 23.6 | 23.7 | 23.5 |
| pelvic origin | 47.0 | 47.0 | 47.0 | 46.2 | 47.6 | 46.4 | 48.0 | 50.4 | 48.6 | 48.2 |
| 1st dorsal origin | 32.8 | 32.4 | 32.8 | 32.3 | 33.1 | 32.6 | 33.1 | 34.0 | 32.4 | 33.0 |
| 2nd dorsal origin | 64.6 | 65.4 | 64.7 | 64.4 | 63.8 | 64.3 | 66.2 | 69.2 | 66.0 | 69.1 |
| anal fin origin | 60.4 | 61.3 | 61.2 | 60.5 | 60.9 | 61.4 | 63.0 | 66.1 | 63.2 | 65.4 |
| upper caudal origin | 76.3 | 75.6 | 75.9 | 74.6 | 74.7 | 75.1 | 76.4 | – | 77.0 | 76.5 |
| lower caudal origin | 74.4 | 74.4 | 73.6 | 73.4 | 73.3 | 73.6 | 75.0 | 78.0 | 75.5 | 75.8 |
| Nostrils: | | | | | | | | | | |
| distance between inner corners | 5.2 | 5.0 | 5.2 | 5.2 | 4.8 | 5.0 | 4.9 | 4.9 | 4.8 | 4.9 |
| Mouth: | | | | | | | | | | |
| width | 7.1 | 7.0 | 6.6 | 7.1 | 6.8 | 6.8 | 7.0 | 7.5 | 6.8 | 6.9 |
| length | 4.9 | 4.5 | 5.1 | 5.3 | 5.2 | 5.2 | 5.0 | 5.3 | 5.4 | 5.4 |
| Labial furrow lengths: | | | | | | | | | | |
| upper | 2.3 | 2.2 | 2.3 | 2.5 | 2.1 | 2.4 | 2.4 | 2.4 | 2.2 | 2.6 |
| lower | 1.6 | 1.4 | 1.4 | 1.8 | 1.8 | 1.7 | 1.7 | 1.7 | 1.7 | 1.6 |
| Gill-opening lengths: | | | | | | | | | | |
| 1st | 2.0 | 2.1 | 1.6 | 1.9 | 1.9 | 2.1 | 1.9 | 2.1 | 1.8 | 1.7 |
| 2nd | 2.2 | 2.2 | 2.0 | 2.1 | 2.3 | 2.2 | 2.2 | 2.4 | 2.2 | 2.1 |
| 3rd | 2.3 | 2.2 | 2.2 | 2.2 | 2.6 | 2.1 | 2.4 | 2.4 | 2.4 | 2.4 |
| 4th | 2.1 | 2.2 | 2.3 | 2.1 | 2.6 | 2.3 | 2.5 | 2.7 | 2.5 | 2.3 |
| 5th | 1.6 | 1.7 | 1.6 | 1.7 | 2.1 | 1.8 | 1.9 | 2.0 | 1.8 | 1.6 |
| Eye: | | | | | | | | | | |
| horizontal diameter | 2.7 | 2.9 | 2.9 | 2.5 | 2.3 | 2.3 | 2.1 | 2.3 | 2.1 | 2.0 |
| 1st dorsal fin: | | | | | | | | | | |
| length of base | 9.1 | 9.5 | 9.1 | 9.6 | 8.3 | 8.7 | 9.4 | 9.4 | 9.9 | 8.8 |
| posterior margin | 4.1 | 3.9 | 3.7 | 3.9 | 4.6 | 5.0 | 3.9 | 3.6 | 3.8 | 4.9 |
| height | 7.5 | 7.5 | 7.8 | 7.5 | 8.1 | 8.4 | 8.2 | 8.3 | 8.6 | 9.2 |
| 2nd dorsal fin: | | | | | | | | | | |
| length of base | 3.0 | 2.8 | 2.5 | 3.0 | 2.7 | 2.9 | 2.4 | 2.9 | 3.2 | 2.5 |
| posterior margin | 4.4 | 4.5 | 4.4 | 4.3 | 4.7 | 5.0 | 4.8 | 4.3 | 4.6 | 5.3 |
| height | 1.9 | 2.0 | 1.6 | 1.6 | 1.6 | 1.7 | 1.8 | 2.0 | 2.3 | 1.5 |
| Anal fin: | | | | | | | | | | |
| length of base | 4.4 | 5.1 | 4.5 | 4.4 | 4.1 | 4.3 | 4.2 | 4.6 | 4.4 | 3.6 |
| posterior margin | 3.8 | 3.6 | 3.5 | 3.4 | 4.4 | 4.4 | 4.1 | 4.1 | 4.1 | 4.7 |
| height | 2.7 | 2.8 | 2.5 | 2.7 | 2.7 | 2.7 | 2.7 | 2.8 | 2.6 | 2.7 |
| Pectoral fin: | | | | | | | | | | |
| length of base | 4.5 | 5.3 | 4.9 | 5.0 | 4.8 | 5.2 | 5.1 | 5.3 | 5.1 | 5.3 |
| length of anterior margin | 12.0 | 11.7 | 12.2 | 11.7 | 12.6 | 12.8 | 12.8 | 13.8 | 13.4 | 14.4 |
| length of distal margin | 8.4 | 8.4 | 8.7 | 8.9 | 9.5 | 9.6 | 10.0 | 11.9 | 10.8 | 11.4 |
| width | 8.0 | 8.1 | 8.7 | 7.9 | 7.7 | 8.5 | 7.5 | 8.8 | 8.3 | 8.7 |
| Pelvic fin: | | | | | | | | | | |
| length of base | 4.4 | 4.5 | 4.2 | 4.1 | 4.1 | 4.1 | 4.5 | 4.8 | 5.5 | 4.9 |
| length of anterior margin | 5.0 | 5.0 | 4.7 | 4.7 | 5.0 | 4.8 | 4.6 | 5.0 | 4.6 | 5.2 |
| length of distal margin | 3.6 | 3.6 | 3.6 | 4.0 | 3.9 | 4.2 | 4.1 | 4.7 | 4.2 | 4.0 |
| length of claspers | 2.2 | – | 2.1 | 2.4 | – | – | 3.8 | – | 7.3 | 9.7 |
| Caudal fin: | | | | | | | | | | |
| length of upper lobe | 25.2 | 25.2 | 24.4 | 25.6 | 23.6 | 25.4 | 23.5 | – | 23.6 | 23.9 |
| length of lower lobe | 8.6 | 9.5 | 8.9 | 9.3 | 9.7 | 10.2 | 10.5 | 10.2 | 10.5 | 10.2 |
| length from tip to notch | 6.3 | 6.4 | 5.7 | 6.0 | 5.8 | 5.1 | 6.6 | 6.5 | 6.2 | 5.6 |
| notch depth | 3.3 | 3.9 | 3.8 | 3.3 | 3.6 | 3.9 | 2.9 | 2.9 | 2.8 | 3.6 |

[1] Syntypes of *Carcharias longurio*.

dentition of mature males and females similar; sometimes cusps of teeth of mature males slightly more erect than in females; enlarged hyomandibular pores 8–15 on each side of head.

Denticles imbricate, 3-ridged in young and adults, 3-toothed in young, 3-toothed or irregularly margined in adults.

Color of preserved specimens variable: Body slate or purplish gray, or gray brown above, pale below. Pectorals dark with a pale distal edge, pelvics and anal pale or dusky; upper caudal lobe with a dark margin on dorsal and ventral edges in young; edging on ventral margin absent in adults; lower caudal lobe without dark edging; first and second dorsal fins dusky with posterior margin pale in adults, pale or dark-margined in young.

A low interdorsal ridge present in all specimens examined. Both precaudal pits present, the upper better developed.

Growth changes: There is a general tendency for distance from snout tip to outer nostrils, eye, mouth, and pectoral origin to decrease in percent of t.l. with increased t.l. Distance between inner corners of nostrils and eye diameter also decrease in a similar manner. Distances from snout tip to pelvic, second dorsal, and anal origins tend to increase in percent of t.l. with increased t.l., as do first dorsal height, posterior margin of anal fin, anterior and distal margins of pectoral fin, and length of lower caudal lobe.

In large specimens there is a tendency for the axis of the upper caudal lobe to become raised in relation to the horizontal axis of the body.

Too little information is available to establish the size at which males first mature, but based on the following tabulation it appears that this size is greater than 583 mm.:

| *Locality* | *T.L.* | *Clasper Length (%)* | *Locality* | *T.L.* | *Clasper Length (%)* |
|---|---|---|---|---|---|
| Mexico | 351 | 2.2 | Panama | 583 | 3.8 |
| Mexico | 388 | 2.3 | Peru | 688 | 7.4 |
| Mexico | 402 | 2.1 | Panama | 702 | 8 5 |
| Mexico | 402 | 2.2 | Mexico | 792 | 9.2 |
| Mexico | 402 | 2.0 | Mexico | 916 | 7.1 |
| Mexico | 418 | 2.4 | | | |

The smallest non-embryo seen was 351 mm. and the largest embryo, 300 mm. Hubbs and McHugh (1950) reported free-living specimens as small as 343 mm. and embryos as large as 327 mm. The largest specimen seen was 916 mm., but five embryos are indicated as having been taken from a 1540 mm. female from Peru (Hildebrand, 1946).

The five sibling embryos mentioned above have precaudal vertebral counts of 79, 81, 82, 83, and 86, a range of 8 vertebrae. The known range of variation for the species covers a span of only 19 vertebrae.

I have noted no geographic variation in any character studied.

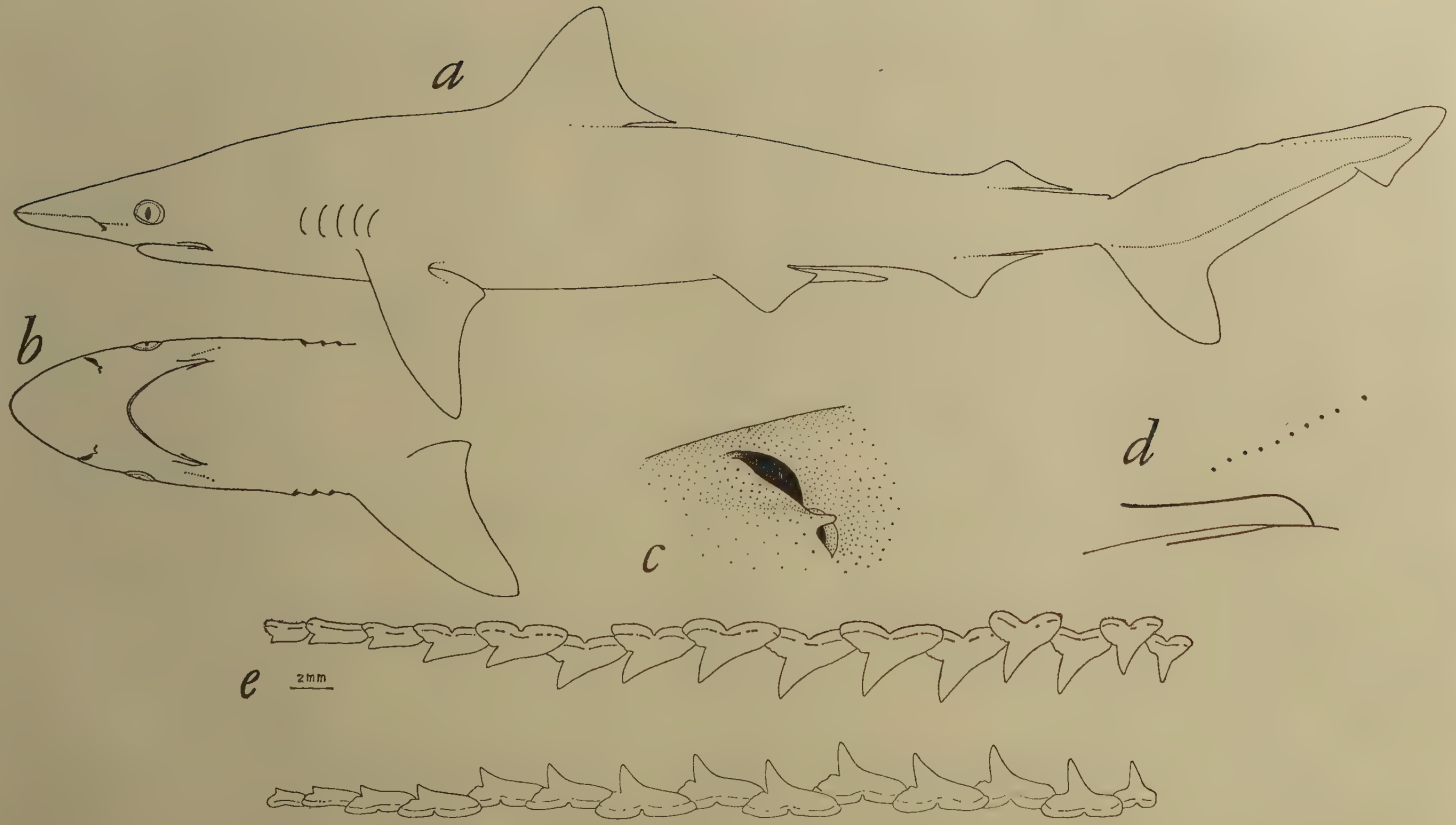


FIGURE 9.—*Rhizoprionodon longurio*, USNM 127756, 688 mm. t.l., mature male from Peru: *a*, left side; *b*, underside of head; *c*, enlarged left nostril; *d*, enlarged left labial furrows and adjacent enlarged hyomandibular pores; *e*, USNM 127756, 657 mm. t.l., female from Peru, right upper and lower teeth (symphysis to the right; base line refers only to teeth).

DISTRIBUTION.—Eastern Pacific Ocean from Peru to southern California, from waters as deep as 15 fathoms.

RELATIONSHIPS.—Within the subgenus *Rhizoprionodon*, *R. longurio* forms a separate offshoot from the remaining three species, differing mainly in its high tooth counts, long snout, and upper labial furrow lengths.

MATERIAL.—MEXICO: Baja California: San Juanico Bay, USNM 196122 (1: 388 mm.), USNM 190594 (2: 402–403), UCLA W52–246 (12: 385–466), SIO H51–306 (2: 351–358); Concepción Bay, USNM 46852 (1: 916); beach one-half mile south of San Felipe, USNM 190590 (1: 385); Sonora: Salinas Bay, SU 17329 (2: 398–460); Mazatlán, USNM 28306 (1: 517, syntype of *Carcharias longurio*), USNM 28330 (1: 792, syntype of *Carcharias longurio*), USNM 29551 (1: 518, syntype of *Carcharias longurio*), SU 11594 (1: ca. 685). PANAMA: NMV [no number] (1: 525); 1–3 miles southeast of Isla Taboga, 2–4 miles off Río Pacora, UCLA W53–273 (4: 301–349); Panama City, USNM 78101 (1: 583); Panama City, fish market, USNM 79291 (1: 702). PERU: Gulf of Guayaquil: 81°13′ W. and 4°13′ S., USNM 127756 (2: 657–688); off Mt. Organos, Cabo Blanco, USNM 127776 (5: 282–300, embryos from 1540 mm. female).

### *Rhizoprionodon (Protozygaena) lalandei* Valenciennes

FIGURES 10, 11; PLATE 2B

*Carcharias* (*Scoliodon*) *lalandii* Valenciennes *in* Müller and Henle, 1841, Systematische Beschreibung der Plagiostomen, p. 30 (Rio de Janeiro, Martinique, Guadeloupe).

*Scoliodon intermedius* Garman, 1913, Mem. Mus. Comp. Zool., vol. 36 (text), p. 115 (Philippines, East Indies).

DIAGNOSIS.—Upper labial furrow well developed, 1.4–2.1 percent of t.l.; precaudal centra slightly elongate in posterior monospondylous region (plate 2B); precaudal vertebrae greater in number than caudal vertebrae; anterior margin of pectoral fin shorter than total length of first dorsal fin (equal to, in 1 out of 33 specimens); snout in front of nostrils 4.4–5.1 percent of t.l. in specimens less than 575 mm. t.l., 4.4–4.7 percent of t.l. in specimens over 575 mm. t.l.; total teeth in outer row of upper jaw 25; total teeth in outer row of lower jaw 24 (23 in 2 out of 21 specimens); total enlarged hyomandibular pores on both sides of head usually more than 16 (25 out of 26 specimens); first dorsal origin usually over level of appressed pectoral inner corner, ranging to just behind inner corner; origin of second dorsal fin usually over anal axil but may occur as far forward as above posterior fourth of anal base; tip of appressed pectoral fin reaches to below level of anterior third or less of first dorsal base. Males maturing at about 500 mm.

DESCRIPTION (see table 15).—Precaudal vertebrae 79–90 (only 4 specimens out of 45 with less than 85); caudal vertebrae 67–79;

TABLE 15.—*Proportional dimensions in percent of total length of* Rhizoprionodon lalandei

| | ♂352 mm. Suri-nam USNM 196134 | ♀366 mm. Suri-nam USNM 196134 | ♂370 mm. Suri-nam USNM 196133 | ♂390 mm. Suri-nam USNM 196134 | ♂446 mm. Brazil SU 14049 | ♀501 mm. MCZ 485[1] | ♂503 mm. Vene-zuela USNM 127099 | ♂519 mm. Vene-zuela USNM 127099 | ♀612 mm. Vene-zuela USNM 127099 |
|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | |
| outer nostrils | 4.7 | 4.6 | 4.9 | 4.6 | 4.8 | 4.6 | 4.7 | 4.8 | 4.7 |
| eye | 8.2 | 8.0 | 8.4 | 8.1 | 8.3 | 7.4 | 7.9 | 8.0 | 8.0 |
| mouth | 8.7 | 8.7 | 8.8 | 8.6 | 8.3 | 7.8 | 8.3 | 8.5 | 8.2 |
| 1st gill-opening | 18.2 | 18.8 | 18.9 | 18.0 | 18.6 | 17.9 | 18.5 | 19.1 | 19.1 |
| pectoral origin | 21.0 | 20.8 | 21.9 | 21.0 | 21.8 | 21.3 | 21.7 | 22.2 | 22.6 |
| pelvic origin | 43.8 | 44.6 | 45.6 | 45.2 | 45.8 | 45.6 | 46.2 | 46.0 | 48.0 |
| 1st dorsal origin | 30.7 | 31.2 | 31.1 | 31.0 | 30.3 | 29.9 | 32.4 | 31.4 | 32.4 |
| 2nd dorsal origin | 62.2 | 63.6 | 64.0 | 63.6 | 63.7 | 65.0 | 65.8 | 65.7 | 67.3 |
| anal fin origin | 59.1 | 59.8 | 60.0 | 59.2 | 60.1 | 61.6 | 61.7 | 61.7 | 63.0 |
| upper caudal origin | 74.4 | 74.3 | 75.4 | 74.9 | 75.4 | 75.2 | 76.0 | 76.1 | 77.3 |
| lower caudal origin | 72.4 | 72.4 | 73.5 | 73.3 | 73.8 | 74.4 | 74.4 | 74.9 | 76.0 |
| Nostrils: | | | | | | | | | |
| distance between inner corners | 5.1 | 4.9 | 4.9 | 5.1 | 5.0 | 4.8 | 4.8 | 4.9 | 4.9 |
| Mouth: | | | | | | | | | |
| width | 6.4 | 6.1 | 6.4 | 6.2 | 6.4 | 6.4 | 6.7 | 7.0 | 7.2 |
| length | 4.5 | 4.4 | 4.6 | 4.1 | 4.5 | 4.5 | 4.9 | 5.0 | 5.2 |
| Labial furrow lengths: | | | | | | | | | |
| upper | 1.5 | 1.7 | 1.5 | 1.6 | 1.8 | 1.8 | 1.7 | 1.8 | 1.6 |
| lower | 1.2 | 1.1 | 1.2 | 1.6 | 1.4 | 1.5 | 1.3 | 1.7 | 1.5 |
| Gill-opening lengths: | | | | | | | | | |
| 1st | 1.6 | 1.5 | 1.8 | 1.5 | 1.8 | 1.4 | 1.4 | 1.7 | 1.6 |
| 2nd | 1.9 | 1.8 | 1.9 | 1.9 | 2.1 | 1.6 | 1.8 | 2.0 | 1.9 |
| 3rd | 2.2 | 1.9 | 2.0 | 2.2 | 2.3 | 1.9 | 1.9 | 2.2 | 2.1 |
| 4th | 2.3 | 2.1 | 2.1 | 2.1 | 2.2 | 1.9 | 2.0 | 2.2 | 2.2 |
| 5th | 2.0 | 1.4 | 1.8 | 1.8 | 1.7 | 1.6 | 1.6 | 1.7 | 1.6 |
| Eye: | | | | | | | | | |
| horizontal diameter | 2.7 | 2.3 | 2.7 | 2.4 | 2.2 | 2.1 | 2.4 | 2.5 | 2.1 |
| 1st dorsal fin: | | | | | | | | | |
| length of base | 9.3 | 9.6 | 9.1 | 9.5 | 9.7 | 8.4 | 9.4 | 10.0 | 10.8 |
| posterior margin | 4.3 | 4.4 | 4.5 | 4.6 | 4.8 | 5.2 | 4.2 | 4.2 | 4.4 |
| height | 7.1 | 7.2 | 6.9 | 7.2 | 8.1 | 8.2 | 8.3 | 8.1 | 8.2 |
| 2nd dorsal fin: | | | | | | | | | |
| length of base | 2.4 | 2.7 | 2.4 | 2.8 | 2.4 | 2.3 | 2.4 | 2.4 | 2.5 |
| posterior margin | 4.3 | 4.3 | 4.1 | 4.6 | 5.0 | 4.7 | 4.7 | 4.8 | 5.0 |
| height | 1.7 | 1.6 | 1.7 | 1.7 | 1.7 | 1.8 | 1.6 | 1.8 | 1.9 |
| Anal fin: | | | | | | | | | |
| length of base | 4.5 | 4.3 | 4.5 | 4.9 | 4.8 | 4.1 | 4.3 | 4.4 | 4.4 |
| length of posterior margin | 3.6 | 3.9 | 3.9 | 3.7 | 4.5 | 3.9 | 3.8 | 4.1 | 4.2 |
| height | 2.2 | 2.3 | 2.4 | 2.3 | 2.6 | 2.8 | 2.4 | 2.5 | 2.6 |
| Pectoral fin: | | | | | | | | | |
| length of base | 5.2 | 4.9 | 5.1 | 4.9 | 5.2 | 5.1 | 5.0 | 5.3 | 5.4 |
| length of anterior margin | 11.1 | 11.6 | 11.1 | 11.6 | 12.9 | 12.8 | 11.9 | 12.2 | 12.9 |
| length of distal margin | 7.9 | 7.9 | 7.7 | 7.4 | 9.8 | 9.1 | 9.4 | 9.7 | 9.9 |
| width | 7.5 | 7.3 | 7.5 | 7.4 | 8.9 | 8.3 | 8.1 | 8.1 | 8.4 |
| Pelvic fin: | | | | | | | | | |
| length of base | 4.3 | 4.2 | 4.0 | 4.0 | 4.0 | 4.1 | 4.4 | 4.5 | 4.5 |
| length of anterior margin | 4.4 | 4.6 | 4.6 | 4.5 | 4.7 | 4.6 | 4.6 | 4.6 | 4.7 |
| length of distal margin | 3.7 | 3.8 | 3.6 | 3.7 | 4.3 | 4.3 | 3.8 | 4.4 | 4.6 |
| length of claspers | 2.2 | – | 2.6 | 2.2 | 3.3 | – | 7.1 | 7.4 | – |
| Caudal fin: | | | | | | | | | |
| length of upper lobe | 25.3 | 26.5 | 25.3 | 24.9 | 25.7 | 25.1 | 24.7 | 24.9 | 23.6 |
| length of lower lobe | 9.2 | 9.6 | 10.0 | 9.5 | 9.6 | 10.6 | 9.8 | 9.6 | 9.5 |
| length from tip to notch | 5.4 | 6.0 | 5.4 | 5.4 | 6.3 | 6.8 | 5.9 | 6.5 | 6.0 |
| notch depth | 4.0 | 4.1 | 4.0 | 4.1 | 4.0 | 3.2 | 3.8 | 3.8 | 3.6 |

[1] Lectotype of *Scoliodon intermedius*.

total vertebrae 153–168; upper teeth 12–1–12; lower teeth 11–12 to 12–12 (usually 12–12); cusps of teeth smooth to faintly irregular, posterior margins sometimes denticulate; anterior teeth of lower jaw of mature males distinct from those of females and young males (fig. 11); in mature males cusps of anterior teeth of lower jaw are slenderer and rounder in cross section than in females and young males. This situation is somewhat analagous to, but less striking than, that found in *Scoliodon* (p. 578). Enlarged hyomandibular pores 6–14 (rarely less than 8, usually 10 or 11) on each side of head.

Denticles imbricate (adults), 3-ridged and 3-toothed in young, 3- to 5-ridged and 3- to 5-toothed or irregularly margined in adults.

Color of preserved specimens: Body slate gray or brownish gray above, pale below; pectorals dusky with a pale distal margin (one young specimen had a blackish diffuse blotch near the tip of each pectoral); pelvics and anal pale or light dusky; caudal dusky or with a pale area centrally on each side; posterior margin of upper and lower lobes black-edged; first dorsal dusky with or without a pale posterior margin; second dorsal dusky. Distal portion of clasper of adult male sometimes abruptly paler than remainder.

A low interdorsal ridge present in well-preserved specimens. Both precaudal pits present, the upper better developed.

Growth changes: There is a slight tendency for distance from snout tip to outer nostrils, eye, and mouth to decrease in percent of t.l. with increased t.l. Length of upper lobe of caudal fin and caudal notch depth also decrease in similar manner. Distance from snout tip to pelvic, second dorsal, anal, and upper and lower caudal origins increase in percent of t.l. with increased t.l., as do also mouth width and length, first dorsal height, anal height, anterior and distal margins of pectoral fin, and width of pectoral fin.

In large specimens there is a tendency for the axis of the upper caudal lobe to become raised in relation to the horizontal axis of the body.

On the basis of the following tabulation males appear to mature at between 446 and 503 mm.:

| *Locality* | *T.L.* | *Clasper Length (%)* | *Locality* | *T.L.* | *Clasper Length (%)* |
|---|---|---|---|---|---|
| Brazil | 292 | 2.1 | Brazil | 392 | 2.7 |
| Brazil | 303 | 2.6 | Brazil | 400 | 2.8 |
| Brazil | 311 | 2.2 | Brazil | 446 | 3.3 |
| Brazil | 324 | 2.6 | Venezuela | 503 | 7.1 |
| Brazil | 338 | 2.0 | Panama | 510 | 5.9 |
| Brazil | 350 | 2.7 | Venezuela | 512 | 7.2 |
| Surinam | 353 | 2.2 | Venezuela | 519 | 7.4 |
| Brazil | 358 | 2.4 | Panama | 538 | 7.1 |
| Surinam | 370 | 2.6 | Brazil | 540 | 5.3 |
| Surinam | 390 | 2.2 | Brazil | 640 | 6.3 |

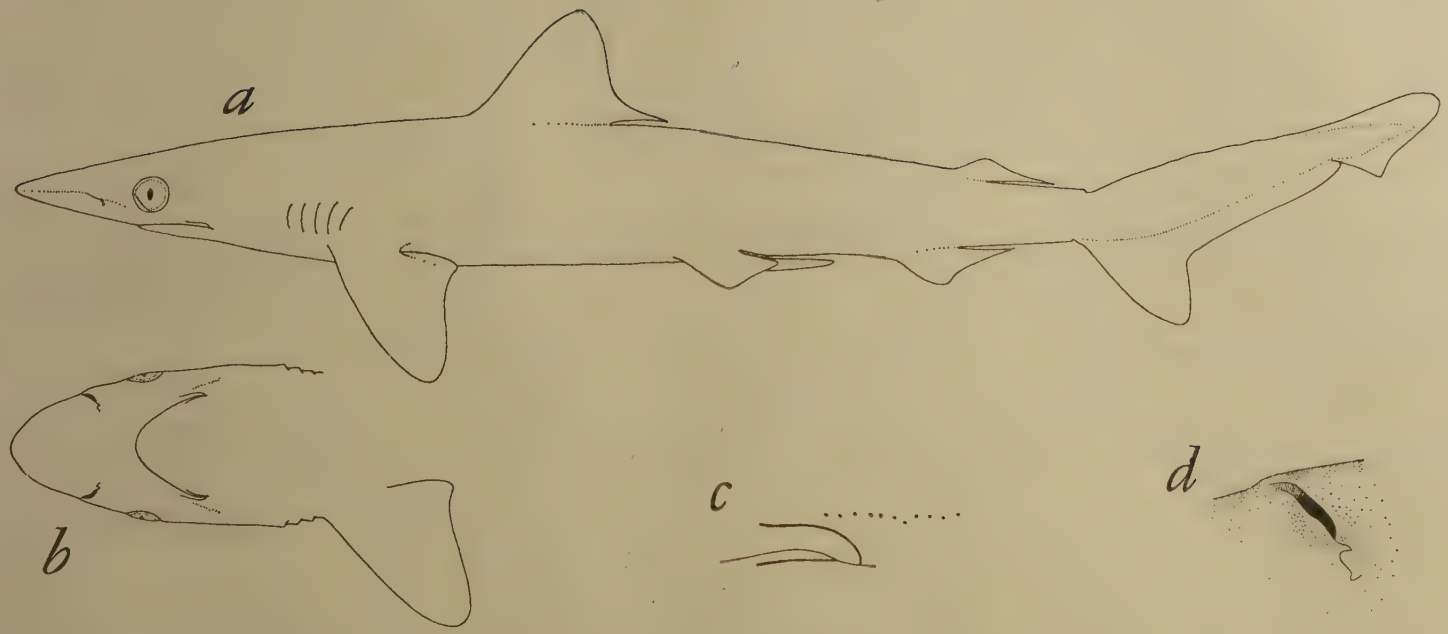


FIGURE 10.—*Rhizoprionodon lalandei*, USNM 127099, 519 mm. t.l., mature male from Venezuela: *a*, left side; *b*, underside of head; *c*, enlarged left labial furrows and adjacent enlarged hyomandibular pores; *d*, enlarged left nostril.

No embryos were seen; the smallest non-embryo examined was 292 mm. and the largest was 640 mm.

DISTRIBUTION.—Western Atlantic continental coasts from Colón, Panama, to Florianopolis, Brazil.

RELATIONSHIPS.—*Rhizoprionodon lalandei* is most closely related to the cognates *R. oligolinx* and *R. taylori*. It differs from them in always having well-developed upper labial furrows (always longer in percent of t.l. than either of the two cognates) and a typically higher tooth count. In addition, it differs from *R. taylori* in having a greater number of precaudal vertebrae and from *R. oligolinx* in having more enlarged hyomandibular pores.

NOMENCLATURAL DISCUSSION.—The type material of *R. lalandei* consists of specimens of two species, *R. porosus* and what is here considered *R. lalandei*. Lectotype designation is made in the material listed below. The lectotype, MNHN 945, has label data indicating only Brazil as the locality from which it was collected and DeLalande as the collector. The Brazilian type locality given by Müller and Henle (1841) is stated specifically to be Rio de Janeiro, but it is not associated with any particular specimen. The Leiden Museum syntype mentioned by Müller and Henle also has only Brazil listed on the label.

The type material of *Scoliodon intermedius* consists of two specimens also belonging to two species. One, 284 mm., is an *R. acutus* from the Philippines. The other, 501 mm., belongs in the subgenus *Protozygaena* and is labeled from the East Indies. The type description is based on a single specimen, obviously the larger of the two, and I designate it here as lectotype (see "Material"). This specimen has longer labial furrows and somewhat longer precaudal centra in the posterior monospondylous region than do *R. taylori* and *R. oligolinx*. Both of these characters, as well as its enlarged hyomandibular pore count of 20 and possibly its precaudal vertebral count (one less than for any specimen of *R. oligolinx*), exclude its being *R. oligolinx*, which is the only member of the subgenus known from the East Indies. Its higher precaudal vertebral count also seems to exclude it from *R. taylori*, which is known only from Australia.

The combination of these critical characters falls in nicely with those of *R. lalandei*. Unless there is another species of the subgenus in the Pacific or the specimen is an aberrant one of either of the two species known from the Pacific, it seems probable that the specimen is *R. lalandei* and that the locality data somehow has been incorrectly recorded.

MATERIAL.—PANAMA: Colón, USNM 79288 (1: 510 mm.), USNM 79290 (1: 538), ANSP 49849 (1: ca. 410). GULF OF VENEZUELA:

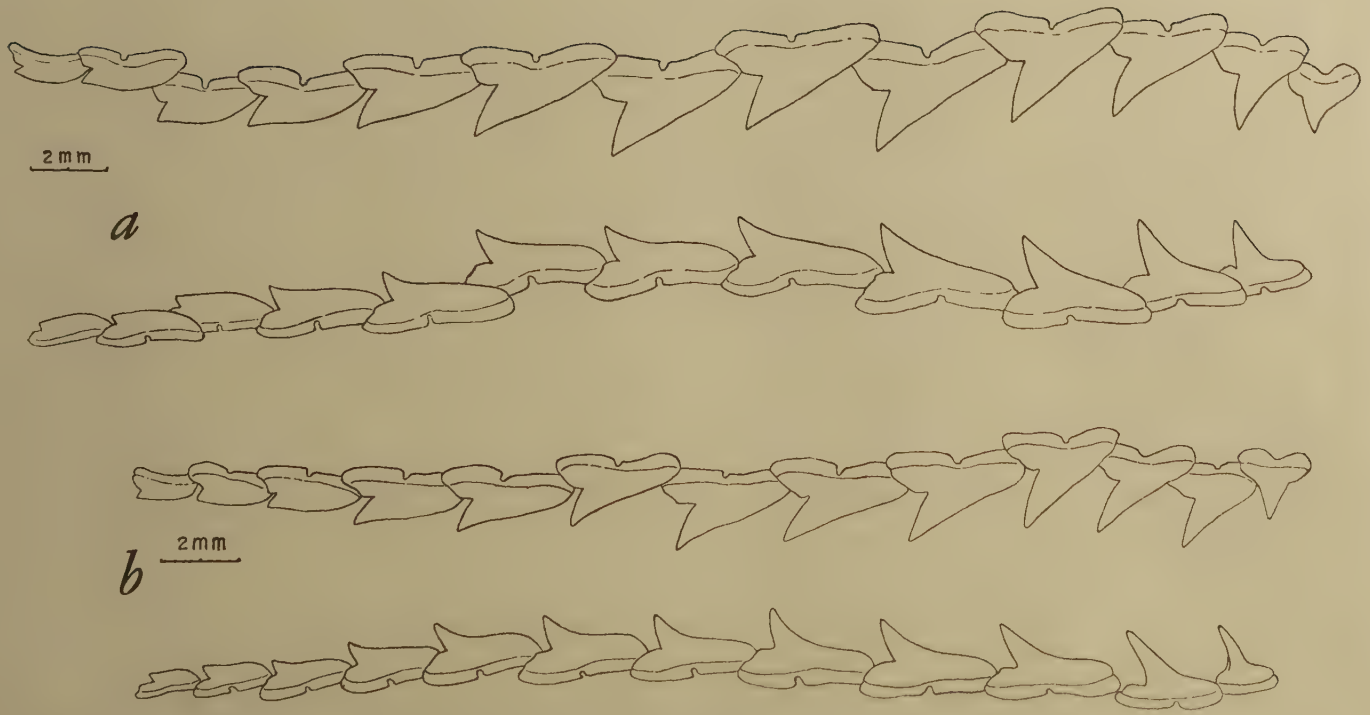


FIGURE 11.—*Rhizoprionodon lalandei*, USNM 127099 from Peru: *a*, 612 mm. t.l., female, right upper and lower teeth (symphysis to the right); *b*, 512 mm. t.l., male, right upper and lower teeth (symphysis to the right).

USNM 127099 (4: 503–612). SURINAM: 6°24′–6°22′ N. and 54°55′–54°59′ W., at 14 fathoms, USNM 196133 (1: 370); 6°21′–6°20.5′ N., and 54°59′–54°54′ W., at 14 fathoms, USNM 196134 (3: 352–390). BRAZIL: MNHN 945 (1: 303, male, here designated lectotype of *Carcharias* (*Scoliodon*) *lalandei*), RNH 4339 (1: 315); Recife, Pernambuco, USNM 104310, (1: 417); Bahía, UZMK 356 (1: 572); Victoria, SU 52749 (1: 640), SU 52853 (1: ca. 330), SU 52854 (1: ca. 365), SU 52856 (4: 292–311); Rio de Janeiro, MCZ 91 (1: 605), ZSZM 8037 (1: ca. 340), NMV [no number] (1: 501), MNHN 1065 (1: 489), BMNH 1903.6.9.130–132 (1: 591); Bandeirantes, USNM 100811 (3: 324–350); south of Ilha Grande, SU 52759 (1: ca. 605); fish market at Rio de Janeiro, SU 52750 (1: ca. 317), SU 52751 (1: 412), SU 52752 (1: 540), SU 52753 (1: 400), SU 52754 (1: 338), SU 52755 (1: 335), SU 52756 (1: 311), SU 52757 (1: 330); Santos, SU 14049 (2: 392–446), CAS 11812 (1: 313); mouth of Rio Itapoca, (1: 358); Florianopolis, Ribeirao, SU 52862 (1: 506). "EAST INDIES" [probably in error]: MCZ 485 (1: 501, here designated lectotype of *Scoliodon intermedius*).

### *Rhizoprionodon* (*Protozygaena*) *oligolinx*, new species

FIGURES 12, 13; PLATE 2c

DIAGNOSIS.—Upper labial furrow poorly developed, 0.0–1.3 percent of t.l. (less than 1.0 percent in 37 out of 45 specimens); precaudal centra not obviously elongate in posterior monospondylous region (plate 2c); precaudal vertebrae greater in number than caudal vertebrae; anterior margin of pectoral fin shorter than total length of first dorsal fin; snout in front of nostrils 3.7–4.7 percent of total length (only 3 specimens over 575 mm. seen and snout length of only 1 of these was measured, 610 mm., 3.9 percent); total teeth in outer row of upper jaw 23–25 (23 in 30 out of 55 specimens); total teeth in outer row of lower jaw 21–24 (22 in 42 out of 55 specimens); total enlarged hyomandibular pores on both sides of head usually less than 16 (55 out of 56 specimens); first dorsal origin over, or just posterior to, level of appressed pectoral inner corner; origin of second dorsal fin usually over a point just in advance of anal axil, but may occur as far forward as above posterior third of anal base; tip of appressed pectoral fin reaches to below level of anterior third or less of first dorsal base. Males maturing at less than 380 mm.

DESCRIPTION (see table 16).—Precaudal vertebrae 84–91 (only 1 specimen each, out of 54, with 84 and 91); caudal vertebrae 64–75; total vertebrae 151–162; cusps of teeth smooth to faintly irregular; posterior margins sometimes denticulate; anterior teeth of lower jaw of mature males distinct from those of females and young males

TABLE 16.—*Proportional dimensions in percent of total length of* Rhizoprionodon oligolinx

| | ♂272 mm. India USNM 175349 | ♂276 mm. India SU 41981 | ♀315 mm. Thailand ANSP 60403 | ♀395 mm. Malaya MCZ 180 | ♂400 mm. Java UMMZ 177113 | ♂413 mm. Thailand ZSZM 7533 | ♀417 mm. Malaya SU 14197 | ♂435 mm. Java UMMZ 177113 | ♀458 mm. Malaya MCZ 111 | ♂489 mm. Thailand USNM 196799 [1] |
|---|---|---|---|---|---|---|---|---|---|---|
| Snout tip to: | | | | | | | | | | |
| outer nostrils | 4.5 | 4.7 | 4.7 | 4.5 | 4.4 | 4.4 | 4.6 | 4.6 | 4.4 | 4.1 |
| eye | 7.5 | 8.2 | 7.7 | 7.5 | 7.2 | 7.2 | 7.6 | 7.4 | 6.8 | 7.0 |
| mouth | 8.1 | 8.3 | 8.2 | 7.7 | 7.5 | 7.8 | 8.0 | 7.7 | 7.2 | 7.3 |
| 1st gill-opening | 19.9 | 18.1 | 18.1 | 18.0 | 18.0 | 18.2 | 17.3 | 17.7 | 16.4 | 16.8 |
| pectoral origin | 23.2 | 21.8 | 21.2 | 20.8 | 21.8 | 22.0 | 21.1 | 20.9 | 19.6 | 20.8 |
| pelvic origin | 45.6 | 44.5 | 45.7 | 46.0 | 45.0 | 46.2 | 46.6 | 46.0 | 45.0 | 46.0 |
| 1st dorsal origin | 33.1 | 31.9 | 31.8 | 31.6 | 30.2 | 31.7 | 31.2 | 31.7 | 30.1 | 30.8 |
| 2nd dorsal origin | 63.3 | 62.3 | 63.8 | 63.8 | 63.3 | 65.4 | 65.0 | 64.2 | 63.2 | 65.5 |
| anal origin | 59.2 | 58.7 | 59.4 | 60.2 | 60.0 | 61.2 | 61.2 | 61.4 | 59.0 | 61.5 |
| upper caudal origin | 73.2 | 74.3 | 74.0 | 73.9 | 74.6 | 76.0 | 74.8 | 75.2 | 74.5 | 76.6 |
| lower caudal origin | 72.5 | 71.7 | 72.5 | 72.4 | 73.3 | 74.4 | 74.1 | 73.6 | 72.7 | 75.0 |
| Nostrils: | | | | | | | | | | |
| distance between inner corners | 5.5 | 5.1 | 5.1 | 4.3 | 4.8 | 4.5 | 4.6 | 4.8 | 4.5 | 4.5 |
| Mouth: | | | | | | | | | | |
| width | 7.2 | 7.1 | 7.7 | 6.5 | 7.0 | 6.5 | 6.9 | 6.6 | 6.6 | 7.1 |
| length | 5.3 | 5.1 | 4.6 | 5.1 | 4.9 | 5.0 | 4.4 | 4.8 | 4.9 | 4.8 |
| Labial furrow lengths: | | | | | | | | | | |
| upper | 0.7 | 0.6 | 0.5 | 0.2 | 0.5 | 0.5 | 0.5 | 0.9 | 0.3 | 0.3 |
| lower | 1.4 | 1.5 | 1.4 | 1.5 | 1.4 | 1.4 | 1.3 | 1.4 | 1.4 | 1.3 |
| Gill-opening lengths: | | | | | | | | | | |
| 1st | 1.9 | 1.7 | 1.7 | 1.5 | 1.6 | 1.6 | 1.4 | 1.6 | 1.7 | 1.9 |
| 2nd | 2.2 | 2.0 | 1.9 | 1.7 | 2.0 | 1.8 | 1.7 | 1.8 | 1.7 | 2.4 |
| 3rd | 2.3 | 2.2 | 2.1 | 1.8 | 2.2 | 1.9 | 1.9 | 2.2 | 2.1 | 2.6 |
| 4th | 2.4 | 2.5 | 2.3 | 2.0 | 2.4 | 2.2 | 2.1 | 2.4 | 2.1 | 2.7 |
| 5th | 2.0 | 2.1 | 2.0 | 1.8 | 1.8 | 1.9 | 1.8 | 2.1 | 1.6 | 2.3 |
| Eye: | | | | | | | | | | |
| horizontal diameter | 3.2 | 3.0 | 2.8 | 2.2 | 2.2 | 2.4 | 2.2 | 2.3 | 2.1 | 2.1 |
| 1st dorsal fin: | | | | | | | | | | |
| length of base | 9.8 | 9.5 | 10.0 | 9.5 | 9.7 | 9.0 | 9.2 | 9.6 | 10.1 | 10.1 |
| posterior margin | 4.2 | 4.3 | 5.0 | 4.7 | 4.8 | 4.5 | 4.9 | 4.8 | 5.1 | 3.9 |
| height | 8.3 | 8.0 | 7.9 | 8.6 | 7.9 | 7.6 | 7.3 | 8.1 | 8.5 | 8.0 |
| 2nd dorsal fin: | | | | | | | | | | |
| length of base | 2.2 | 2.9 | 2.2 | 2.7 | 2.8 | 2.4 | 2.4 | 2.9 | 2.4 | 2.5 |
| posterior margin | 5.1 | 5.0 | 5.5 | 5.3 | 5.2 | 5.2 | 5.0 | 5.1 | 5.1 | 4.7 |
| height | 1.7 | 1.7 | 1.7 | 1.8 | 1.6 | 1.9 | 1.7 | 1.6 | 1.9 | 1.6 |
| Anal fin: | | | | | | | | | | |
| length of base | 4.8 | 5.2 | 4.8 | 4.7 | 4.8 | 5.1 | 5.1 | 4.8 | 4.8 | 5.0 |
| length of posterior margin | 4.8 | 4.0 | 5.0 | 4.8 | 4.9 | 4.5 | 4.7 | 4.7 | 4.9 | 4.3 |
| height | 2.7 | 2.9 | 2.7 | 3.1 | 2.6 | 2.7 | 2.7 | 2.7 | 2.9 | 2.4 |
| Pectoral fin: | | | | | | | | | | |
| length of base | 5.3 | 5.5 | 5.3 | 5.3 | 5.6 | 4.9 | 5.9 | 5.1 | 5.1 | 5.5 |
| length of anterior margin | 12.4 | 11.8 | 11.7 | 13.3 | 12.2 | 12.2 | 12.0 | 12.4 | 13.1 | 11.7 |
| length of distal margin | 7.9 | 7.3 | 7.6 | 8.4 | 9.2 | 8.2 | 8.4 | 8.4 | 9.1 | 8.0 |
| width | 7.6 | 7.7 | 8.0 | 8.0 | 8.4 | 7.9 | 7.5 | 7.9 | 8.1 | 7.4 |
| Pelvic fin: | | | | | | | | | | |
| length of base | 4.0 | 4.1 | 4.1 | 4.0 | 4.6 | 4.5 | 4.3 | 4.4 | 3.8 | 4.3 |
| length of anterior margin | 5.2 | 4.5 | 5.3 | 5.0 | 4.6 | 4.9 | 4.7 | 4.6 | 5.1 | 4.3 |
| length of distal margin | 4.0 | 4.3 | 3.8 | 4.3 | 4.6 | 4.4 | 4.3 | 4.2 | 3.9 | 3.9 |
| length of claspers | 2.0 | 2.2 | – | – | 8.6 | 8.7 | – | 8.5 | – | 7.7 |
| Caudal fin: | | | | | | | | | | |
| length of upper lobe | 27.2 | 26.6 | 25.1 | 25.9 | 25.4 | 24.6 | 25.8 | 25.2 | 26.4 | 23.5 |
| length of lower lobe | 10.3 | 10.2 | 10.5 | 11.7 | – | 10.1 | 10.1 | 9.8 | 11.4 | 9.6 |
| length from tip to notch | 6.0 | 6.3 | 6.0 | 5.9 | 6.0 | 5.9 | 6.4 | 6.4 | 5.6 | 6.3 |
| notch depth | 4.2 | 4.0 | 4.6 | 3.9 | 3.9 | 3.8 | 3.6 | 3.5 | 3.9 | 3.3 |

[1] Holotype of *Rhizoprionodon oligolinx*.

(fig. 13); in mature males the cusps of the anterior teeth of the lower jaw (and sometimes upper) are slenderer and rounder in cross section than in females and young males. This situation is somewhat analogous, but less striking than that found in *Scoliodon* (p. 578). Enlarged hyomandibular pores 3–8 (usually 4–7) on each side of head.

Denticles imbricate, 3-ridged and 3-toothed in young, 3- to 5-ridged and 3- to 5-toothed or irregularly margined in adults.

Color of preserved specimens: Body slate gray or brownish gray above, pale below; pectorals dusky with a pale margin; pelvics and anal pale or light dusky; caudal uniformly dusky or with a pale area centrally on each side; margins of upper caudal lobe black to dusky-edged; first dorsal with or without a pale or faintly dusky posterior margin; second dorsal dusky. Distal portion of clasper of adult male sometimes abruptly paler than remainder.

Interdorsal ridge, when present, very faint. Both precaudal pits present, the upper better developed.

Growth changes: There is a slight tendency for distance from snout tip to eye, mouth, first gill-opening, and pectoral origin to decrease in percent of t.l. with increased t.l. Eye diameter and caudal notch depth decrease similarly. There is a slight tendency for snout tip to anal origin and upper and lower caudal lobe origins to increase in percent of t.l with increased t.l.

In large specimens there is a tendency for the axis of the upper caudal lobe to become raised in relation to the horizontal axis of the body.

The following tabulation indicates that males have mature claspers at between 287 and 380 mm.; however, in at least one male, 387 mm., with mature claspers, dentition was still sexually undifferentiated.

| *Locality* | *T.L.* | *Clasper Length (%)* | *Locality* | *T.L.* | *Clasper Length (%)* |
|---|---|---|---|---|---|
| Java | 219 | 2.2 | Java | 400 | 8.6 |
| India | 261 | 2.8 | Thailand | 413 | 8.7 |
| India | 272 | 2.6 | Java | 414 | 9.4 |
| India | 272 | 2.0 | Madura Straits | 435 | 9.3 |
| India | 276 | 2.2 | Java | 435 | 8.5 |
| India | 280 | 2.7 | Thailand | 448 | 8.6 |
| Ceylon | 287 | 2.2 | Thailand | 461 | 9.0 |
| Japan | 380 | 9.0 | Thalland | 481 | 8.2 |
| Thailand | 387 | 7.8 | Thailand | 489 | 8.7 |

The smallest non-embryo examined was 219 mm. from Batavia; the largest embryo was 261 mm. from Bombay. An embryo 231 mm. was examined from Batavia indicating variation in size at birth. The largest specimen seen was 610 mm. from Kanara, India.

No information is available on vertebral variation among siblings.

FIGURE 12.—*Rhinoprionodon oligolinx*, USNM 117113, 435 mm, t.l., mature male from Java: *a*, left side; *b*, underside of head; *c*, enlarged right labial furrows with adjacent enlarged hyomandibular pores; *d*, enlarged right nostril.

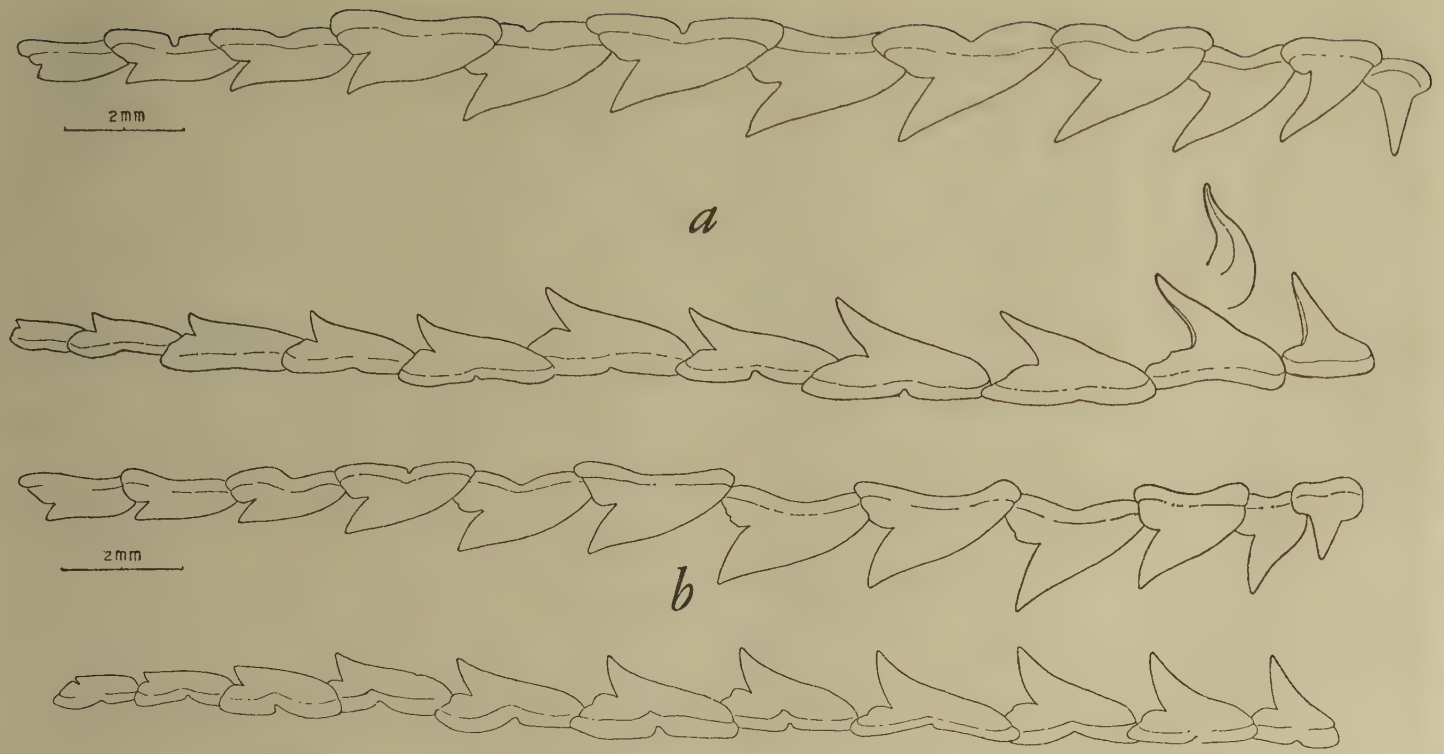


FIGURE 13.—*Rhizoprionodon oligolinx: a*, UMMZ 117113, 400 mm. t.l., mature male from Java, right upper and lower teeth (symphysis to the right; inserted tooth is edge-on view of second lower tooth from the right); *b*, SU 14197, 417 mm. t.l., female from Singapore, right upper and lower teeth (symphysis to the right).

DISTRIBUTION.—From the Persian Gulf, India, Thailand, Malaya, Java, and Madura Straits. One specimen listed from Japan may be an error as no specimens have been identifiably reported from China or the Philippines.

RELATIONSHIPS.—I consider *Rhizoprionodon oligolinx* and *R. taylori* cognate species. *Rhizoprionodon oligolinx* differs from *R. taylori* in having fewer enlarged hyomandibular pores and more precaudal vertebrae. It is also close to *R. lalandei*, from which it is distinguished in having shorter labial furrows, fewer enlarged hyomandibular pores, and typically fewer teeth.

NOMENCLATURAL DISCUSSION.—This species frequently has been called *Scoliodon palasorra*, especially in the Indian literature. I have found that name to be referable to *Scoliodon laticaudus*.

The name "oligolinx" comes from the Greek, meaning "short furrow," and refers to the short upper labial furrow found in this species.

MATERIAL.—Holotype: USNM 196799, 489 mm. male, Gulf of Thailand, ca. 11°56′–12°03′ N. and ca. 102°14′30″–102°17′45″ E., about 2–3 miles offshore, at a depth of 0–10 meters, January 12, 1961, obtained from the Bangkok fish market [information furnished by fisherman; original register number GVF 2467].

Paratypes: PERSIAN GULF: near Hormuz, UZMK CN5 (1: 276 mm.). INDIA: Sind, BMNH 1889.2.1.4150 (1: 594); Bombay, BMNH 1889.2.1.4164–6 (3: 272–608), ANSP 88351 (1: 261, embryo); Alibag, ZSZM H1377 (1: ca. 244), ISH 5/61 (1: 301); Kanara, BMNH 1889.2.1.4175 (1: 610); Coast of Malabar, MNHN A7783 (4: 242–265); Quilon, USNM 175349 (1: 272); Pondicherry, MNHN 946, in part (1: 280); Madras, BMNH 1889.2.1.4161–3 (1: 294); Vizagapatam, BMNH 1868.10.25.21 (1: ca. 260), SU 41981 (1: 276); Calcutta, SU 41986, in part (1: 292). CEYLON: CNHM 58887 (1: 287); 50 miles off coast, NMV [no number], in part (1: ca. 305). GULF OF THAILAND: taken with holotype, GVF 2467 (2: 463–502); ca. 13°09–13′ N. and ca. 100°52–55′ E. GVF 1557 (2: 452–461); ca. 13°20–27′ N. and ca. 100°45′15″–57′ E., GVF 1548 (1: 462); from Chol Buri south to Rayong, GVF 1541 (4: 387–481); Bangkok, ANSP 87215 (1: 220), ANSP 60403 (1: 315), NMV [no number] (1: 391), ISZZ 7533 (1: 413). MALAYA: Singapore, MCZ 180 (1: 395), CNHM 15653 (1: 390), NMV [no number] (1: 226), NMV [no number] (1: ca. 227), SU 14197 (1: 417); Penang, MCZ 111 (1: 458). SUMATRA: Medan, ANSP 77276 (2: 235–260); Padang, ZSZM 10377 (1: 253). JAVA: RNH 4713 (1: 414), MNHN A7772 (1: 407), IRSN 506 (1: 438); Batavia, CNHM 15654 (1: 231, embryo), MCZ 1387 (1: 219); vicinity of Batavia, UMMZ 177113 (3: 250–435). MADURA STRAITS: UZMK 382 (1: 435), UZMK 385 (1: 385). JAPAN: BMNH [no number] (1: 380).

Additional material: EAST INDIAN ARCHIPELAGO: BMNH [no number] (1: 430); USNM 40029 (1: 355; this specimen is listed in the catalog as questionably from Queensland, Australia; I believe it did not come from Australia).

### *Rhizoprionodon* (*Protozygaena*) *taylori* (Ogilby)

FIGURE 14

*Physodon taylori* Ogilby, 1915, Mem. Queensland Mus., vol. 3, p. 117 (Townsville, north Queensland).

DIAGNOSIS.—(Not until this study was in an advanced stage was it realized that *R. taylori* and *R. oligolinx* were separate species; the description that follows is deficient because most of the material examined was not available to me during the writing.) Upper labial furrow poorly developed, 0.7–1.1 percent of t.l.; precaudal centra not obviously elongate in posterior monospondylous region (as in plate 2c); precaudal vertebrae greater in number than caudal vertebrae; anterior margin of pectoral fin shorter than total length of first dorsal fin; snout in front of nostrils 4.0–5.0 percent of t.l. in specimens less than 575 mm. t.l. (5 specimens measured), 4.2 percent of t.l. in specimens over 575 mm. t.l. (2 specimens measured); total teeth in outer row of upper jaw 24–25 (24 in 8 out of 9 specimens); total teeth in outer row of lower jaw 21–23 (22 in 8 out of 9 specimens); total enlarged hyomandibular pores on both sides of head usually more than 16 (6 out of 8 specimens); first dorsal fin origin over level of appressed pectoral inner corner; origin of second dorsal fin ranges from over posterior fourth to over posterior sixth of anal base; tip of appresssed pectoral fin reaches to below level of anterior third or less of first dorsal base. Only two males seen, ca. 310 and 407 mm. t.l., both immature; clasper length in latter 4.8 percent of t.l.

DESCRIPTION (see table 17).—Precaudal vertebrae 73–80; caudal vertebrae 62–70; total vertebrae 135–149; cusps of teeth smooth to faintly irregular; posterior bases sometimes denticulate; enlarged hyomandibular pores 7–11 on each side of head.

Denticles imbricate, 3- to 5-ridged and 3-toothed or irregularly margined (based only on USNM 174075).

Color of preserved specimen (USNM 174075): Body brownish gray above, pale below. Pectorals darker than body color with a pale distal margin; pelvics and anal somewhat lighter than pectorals; caudal paler than body, without black edging on upper lobe; pale posterior edge on lower lobe; first and second dorsal fins about same color as body dorsally.

Interdorsal ridge present or absent. Both precaudal pits present, the upper better developed.

TABLE 17.—*Proportional dimensions in percent of total length of* Rhizoprionodon taylori

| | ♀ 542 mm, Northern Territory AMS IA1611 | ♀ 555 mm, Northern Territory USNM 174075 | ♀ 598 mm, Queensland MCZ 36653 |
|---|---|---|---|
| Snout tip to: | | | |
| outer nostrils | 4.0 | 4.0 | 4.2 |
| eye | 7.1 | 7.3 | 7.1 |
| mouth | 7.4 | 7.3 | 7.1 |
| 1st gill-opening | 17.7 | 16.9 | 17.6 |
| pectoral origin | 21.0 | 20.0 | 20.4 |
| pelvic origin | 45.0 | 46.8 | 44.8 |
| 1st dorsal origin | 31.0 | 30.2 | 29.2 |
| 2nd dorsal origin | 63.7 | 66.0 | 63.7 |
| anal origin | 59.9 | 62.5 | 59.4 |
| upper caudal origin | 76.0 | 77.6 | 75.0 |
| lower caudal origin | 74.6 | 76.4 | 73.7 |
| Nostrils: | | | |
| distance between inner corners | 4.6 | 4.7 | 4.8 |
| Mouth: | | | |
| width | 6.7 | 6.2 | 6.3 |
| length | 4.1 | 4.7 | 4.3 |
| Labial furrow lengths: | | | |
| upper | 0.8 | 0.7 | 0.8 |
| lower | 1.2 | 1.0 | 1.2 |
| Gill-opening lengths: | | | |
| 1st | 1.9 | 1.6 | 1.7 |
| 2nd | 2.2 | 2.0 | 1.9 |
| 3rd | 2.4 | 2.3 | 2.2 |
| 4th | 2.5 | 2.3 | 2.3 |
| 5th | 2.1 | 2.1 | 1.8 |
| Eye: | | | |
| horizontal diameter | 1.7 | 1.9 | 1.9 |
| 1st dorsal fin: | | | |
| length of base | 10.0 | 10.9 | 10.5 |
| posterior margin | 5.0 | 5.8 | 5.2 |
| height | 8.6 | 8.7 | 8.3 |
| 2nd dorsal fin: | | | |
| length of base | 3.0 | 2.8 | 2.8 |
| posterior margin | 4.8 | 5.2 | 4.9 |
| height | 1.9 | 1.9 | 1.8 |
| Anal fin: | | | |
| length of base | 5.3 | 5.0 | 5.2 |
| posterior margin | 4.1 | 4.6 | 4.3 |
| height | 2.4 | 2.6 | 2.8 |
| Pectoral fin: | | | |
| length of base | 4.8 | 6.1 | 5.7 |
| length of anterior margin | 13.0 | 13.9 | 12.9 |
| length of distal margin | 9.4 | 9.1 | 9.0 |
| width | 8.7 | 8.0 | 8.5 |
| Pelvic fin: | | | |
| length of base | 4.6 | 4.9 | 4.9 |
| length of anterior margin | 4.5 | 5.0 | 5.0 |
| length of distal margin | 4.9 | 4.2 | 4.6 |
| length of claspers | – | – | – |
| Caudal fin: | | | |
| length of upper lobe | 24.3 | 23.8 | 25.0 |
| length of lower lobe | 10.0 | 10.3 | 10.2 |
| length from tip to notch | 7.0 | 6.2 | 6.9 |
| notch depth | 3.1 | 3.7 | 3.4 |

FIGURE 14.—*Rhizoprionodon taylori*, USNM 174075, 555 mm. t.l., female from Australia: *a*, left side; *b*, underside of head; *c*, enlarged right nostril; *d*, enlarged right labial furrows and adjacent enlarged hyomandibular pores; *e*, right upper and lower teeth (symphysis to the right; base line refers only to teeth).

All specimens seen were non-embryos and ranged from ca. 310 to ca. 666 mm.

DISTRIBUTION.—Australia from Derby, Western Australia, northward around to south Queensland. The single specimen from Western Australia had 73 precaudal vertebrae while those (9 specimens) from the Northern Territory and Queensland had 77–80. This may indicate some differentiation in the populations.

RELATIONSHIPS.—See under *R. oligolinx* (p. 626).

NOMENCLATURAL DISCUSSION.—Whitley (1940) gave a figure of a specimen that he mistakenly believed to be Ogilby's holotype of *Physodon taylori*. Ogilby (1916) reported his specimen as 657 mm. (Queensland Museum catalog number I12/738) and Whitley illustrated a specimen (I4539, according to Queensland Museum records) approximately 22 inches long, about 4 inches shorter than the holotype. I failed to find the holotype in a search of the Queensland Museum collections, and a note in the museum files indicated that previous efforts to find it had also met with no success.

The nature of the teeth and labial furrows and the position of the anal fin in relation to the second dorsal fin, however, make it certain that Ogilby had a species closely related to *R. oligolinx*. I, therefore, use his name for the only species of such relationship and for which there is no other name available.

MATERIAL.—AUSTRALIA: Western Australia: Derby, AMS IB1551 (1: ca. 390 mm.); Northern Territory: 3.5 miles off Peron Island, QMB I7806 (1: ca. 600); Little Lagoon, Groote Eylandt, Gulf of Carpentaria, USNM 174075 (1: 555); Pellew Islands, Gulf of Carpentaria, AMS IA1611 (1: 542), QMB I3958 (1: 407); Queensland: Cairns, Cooktown Station, MCZ 36653 (1: 598); Townsville, QMB I4539 (1: 522); Salamander Rocks, QMB I6886 (1: 666); Deception Bay, DHMB 45 (1: 323); Burnett River, AMS IB7028 (1: ca. 310).

## Literature Cited


Backus, Richard H.

1957. Notes on western Atlantic sharks. Copeia, 1957, no. 3, pp. 246–248.

Bigelow, Henry B., and Schroeder, W. C.

1948. Sharks, *in* Fishes of the western North Atlantic, part 1. Mem. Sears Found. Mar. Res., no. 1, pp. 59–546.

1957. A study of the sharks of the suborder Squaloidea. Bull. Mus. Comp. Zool., vol. 117, no. 1, pp. 1–150.

Bleeker, Pieter

1852. Bijdrage tot de kennis der Plagiostomen van den Indischen archipel. Verh. Bataviaasch Gen., vol. 24, pp. 1–92.

1853. Bijdrage tot de kennis der Troskieuwige visschen van den Indischen archipel. Verh. Bataviaasch Gen., vol. 25, pp. 1–30.

1878. Quatrieme mémoire sur la faune ichthyologique de la Nouvelle-Guinée. Arch. Neerl. Sci. Nat., vol. 13, pp. 35–66.

1879. Sur quelques espèces inédites ou peu connues de poissons de Chine appartenant au Museum de Hambourg. Verh. Akad. Amsterdam, vol. 18, pp. 1–17.

Cuvier, G. L. F. C. D.

1829. Le Règne animal, 2nd ed., vol. 2, pp. 1–406.

Fowler, Henry W.

1936. The marine fishes of West Africa. Bull. Amer. Mus. Nat. Hist., vol. 70, pt. 1, pp. 1–605.

Garrick, John A. F.

1960. Studies on New Zealand elasmobranchii, part 11: Squaloids of the genera *Deania, Etmopterus, Oxynotus,* and *Dalatias* in New Zealand waters. Trans. Roy. Soc. New Zealand, vol. 88, no. 3, pp. 489–517.

Gill, Theodore N.

1862. Analytical synopsis of the order of Squali; and revision of the nomenclature of the genera. Ann. Lyc. Nat. Hist. New York, vol. 8, pp. 367–413.

Günther, Albert

1870. Catalogue of the fishes in the British Museum, vol. 8, pp. 1–549.

Heath, Gordon W.

1960. The anatomy and growth pattern of the claspers and siphon sacs of the spiny dogfish, *Squalus acanthias* Linnaeus, and the smooth dogfish, *Mustelus canis* Mitchill. Unpubl. doct. dissert., Cornell Univ., 366 pp.

Hildebrand, Samuel F.

1946. A descriptive catalog of the shore fishes of Peru. U.S. Nat. Mus., Bull. 189, pp. 1–530.

Hubbs, Carl L., and McHugh, J. L.

1950. Pacific sharpnose shark (*Scoliodon longurio*) in California and Baja California. California Fish and Game, vol. 36, no. 1, pp. 7–11.

Klausewitz, Wolfgang

1960. Die Typen und Typoide des Naturmuseums Senckenberg, 23: Pisces, Chondrichthyes, Elasmobranchii. Senck. Biol., vol. 41, nos. 5/6, pp. 289–296.

MÜLLER, JOHANNES, and HENLE, F. G. J.
1841. Systematische Beschreibung der Plagiostomen, pp. 1–204, 60 pls.
OGILBY, J. DOUGLAS
1916. Checklist of the cephalochordates, selachians, and fishes of Queensland. Mem. Queensland Mus., vol. 5, pp. 70–98.
RUSSELL, PATRICK
1803. Descriptions and figures of two hundred fishes collected at Vizagapatam on the coast of Coromandel, vol. 1, pp. 1–78, 100 pls.
SETNA, S. B., and SARANGDHAR, P. N.
1949. Descriptions, bionomics and development of *Scoliodon sorrakowah* (Cuvier). Rec. Indian Mus., vol. 46, no. 1, pp. 25–54.
1950. A contribution to the systematics of *Scoliodon acutus* (Rüppell), *Hemipristis elongatus* (Klunzinger) and *Torpedo zugmayeri* Englehart. Rec. Indian Mus., vol. 47, no. 1, pp. 125–134.
SPRINGER, STEWART
1950. A revision of North American sharks allied to the genus *Carcharhinus*. Amer. Mus. Nov., no. 1451, pp. 1–13.
THILLAYAMPALAM, E. M.
1929. *Scoliodon* (the common shark of the Indian seas). Indian Zool. Mem., no. 2, pp. 1–116.
WALTERS, VLADIMIR, and ROBINS, C. RICHARD
1961. A new toadfish (Batrachoididae) considered to be a glacial relict in the West Indies. Amer. Mus. Nov., no. 2047, pp. 1–24.
WHEELER, JOHN F. G.
1959. Sharks of the western Indian Ocean, 1: *Loxodon macrorhinus* M. and H. East African Agric. Journ., vol. 25, no. 2, pp. 106–109.
WHITLEY, GILBERT P.
1940. The fishes of Australia, part 1: The sharks, rays, devil-fish, and other primitive fishes of Australia and New Zealand, pp. 1–280.

U.S. GOVERNMENT PRINTING OFFICE: 1964